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Volume 88

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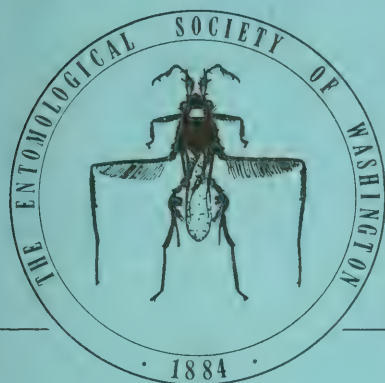
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STANDARD DRAWING CONVENTIONS AND DEFINITIONS FOR VENATIONAL AND OTHER FEATURES OF WINGS OF HYMENOPTERA

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Abstract.—Descriptions of veins and other features of wings in the taxonomic literature of Hymenoptera are usually inadequate, terms are variably applied, and figures are incomplete and not standardized. This situation leads to a deplorable loss of useful taxonomic and phylogenetic information. There is need for standard definitions and some conventions for drawing figures of venational and related features. New terms for three reductional stages of veins are defined: tubular, nebulous and spectral. Flexion lines and folds are defined as well as adventitious veins. A diagrammatical wing section is shown and five kinds of lines representing different venational features presented. Several wings are figured to show examples of the system.

Recent taxonomic works in Hymenoptera often use vague or inadequate terms to describe wing venation and furrows. Figures of wings usually lack details and also lack explanations of conventions used to depict features, resulting in a loss of useful taxonomic characters and making interpretation of such figures a matter of guesswork. This paper is intended to be a plea to hymenopterists writing taxonomic papers to introduce more precision into their descriptions and figures of wings. I wish to make suggestions toward establishing uniform and easily understood definitions and drawing conventions for venational and other features on the wing membrane. Studies of wing anatomy and vein nomenclatural systems can be found elsewhere (Rohwer and Gahan, 1916; Redtenbacher, 1886; Comstock, 1918; Ross, 1936; Carpenter, 1966; Hamilton, 1971-72; Wootton, 1979).

When I refer to veins by name I shall use the Redtenbacher (1886) system as modified by Ross (1936). It is not well known that the hypothesis of homologous venation and the naming scheme for veins that most modern entomologists call the Comstock-Needham system was invented by Redtenbacher (1886), to whom Comstock (1918) rightly gave credit. Redtenbacher's hypothesis of alternating convex and concave veins is now generally accepted, though it was rejected by Comstock, whereas Comstock and Needham's hypothesis that the ontogeny of wing trachea determines the course of veins was subsequently disproven (Wootton, 1979). Comstock's very large production of textbooks and great reputation as a teacher have largely eclipsed Redtenbacher's sound and original contribution.

VEINS AND OTHER FEATURES OF THE WINGS

Although wings of generalized insects have an arrangement of alternating concave and convex veins (Carpenter, 1966), the Hymenoptera have lost all but a

small remnant of the concave veins, leaving almost all members of the order with exclusively convex longitudinal veins. The only obvious concave vein is the subcosta, present in only a few small families of Symphyta. The posterior branch of the radius (Rs) although said to be primitively concave, is convex throughout the Hymenoptera. Media posterior, also a concave vein, is absent.

The cubitus posterior, also concave, is normally absent in Hymenoptera, but it may coincide with the claval flexion line, although often both are distinct in Neuroptera and Plecoptera (Wootton, 1979). One family, the Rhopalosomatidae, has an unsclerotized but strongly pigmented vein in the outer posterior section of the fore wing (Fig. 4, CuP). This vein is concave above and represents, I postulate, the distal part of cubitus posterior extending from near the claval notch to the wing margin. It is the only clear cubitus posterior that I have seen in Hymenoptera. In addition many primitive sphecoids and bees and some ichneumonids and megalyrids have an unpigmented concave crease in exactly the same place (Fig. 5), probably also a trace of CuP. The course of this trace is strongly arcuate and extends no more than half way to the wing margin. Finally, in Cynipoidea, the trace venation of the hind wing has apparently become secondarily concave, a peculiarity of this group. Except for these unusual cases, the venation in Hymenoptera is entirely convex.

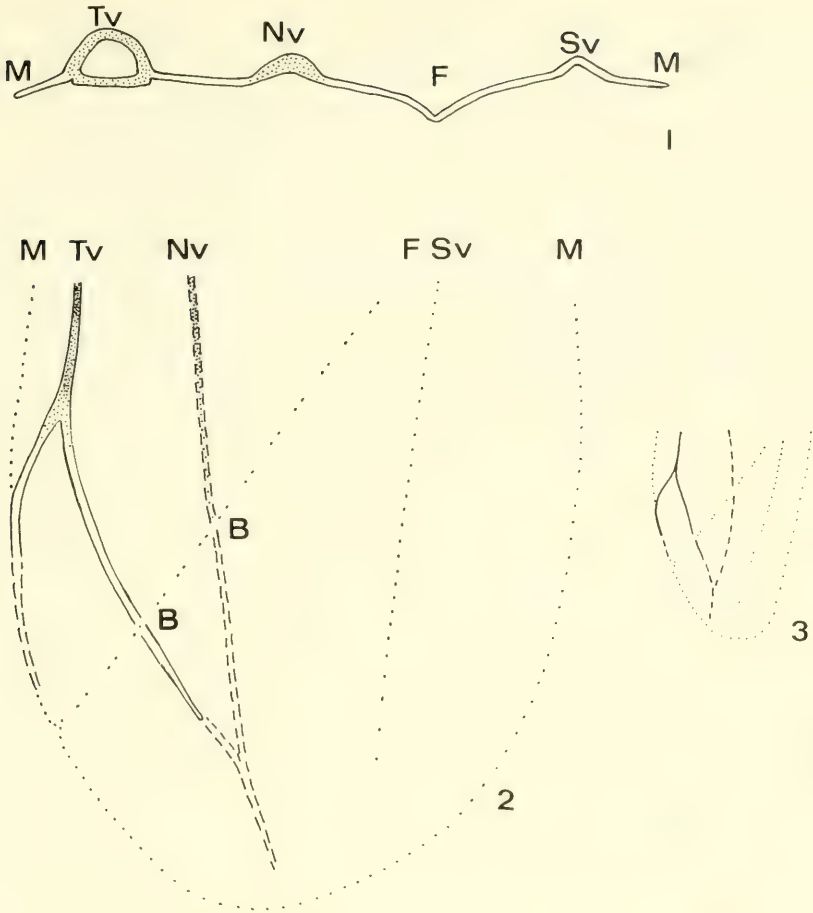
Wing membranes usually also exhibit flexion lines (Wootton, 1979), which are concave above in Hymenoptera (Figs. 1F, 2F) and represent areas of the wing membrane that flex during flight, apparently for aerodynamic reasons. Thus, with rare exceptions, all veins in Hymenoptera are convex above whereas flexion lines are concave. Being concolorous with the membrane, the flexion lines, are almost or quite invisible by transmitted light, and therefore cannot be studied or drawn in this mode of illumination. One must, instead, use diffused light reflected from the wing membrane. I must stress that trace venation (spectral veins—see definition below) and flexion lines cannot be studied from wings placed in mounting medium on a slide or even glued to a slide without a cover slip.

Finally the wings of Neoptera contain fold lines which, as the name suggests, have a function in folding of the wings (Wootton, 1979). In Hymenoptera the only fold line is found in the hind wing where the jugum meets the rest of the wing (Fig. 6). Here it is convex but is of such limited occurrence and so easily identified that it can usually be ignored in taxonomic descriptions.

DEFINITIONS OF REDUCTIONAL STAGES OF VEINS

Stages of reduction of veins.—1. *Tubular vein* (Figs. 1Tv, 2Tv): a rigid tubular structure with sharply defined edges, usually yellow, brown or even black, but sometimes milky or clear. The edges appear darker, the center paler. The normal wing vein of Hymenoptera. These are sometimes called “tracheated” veins but the term is misleading because it has been repeatedly demonstrated that veins are formed independently of tracheae (summarized by Wootton, 1979; Carpenter, 1966).

2. *Nebulous vein* (Figs. 1Nv, 2Nv): a more or less pigmented vein without a tubular structure, thus having ill-defined edges. These veins appear darkest centrally and fade gradually toward the edges. They are visible by transmitted light and also by light reflected from the wing membrane at an angle. The name refers to the cloudy indefinite margins.

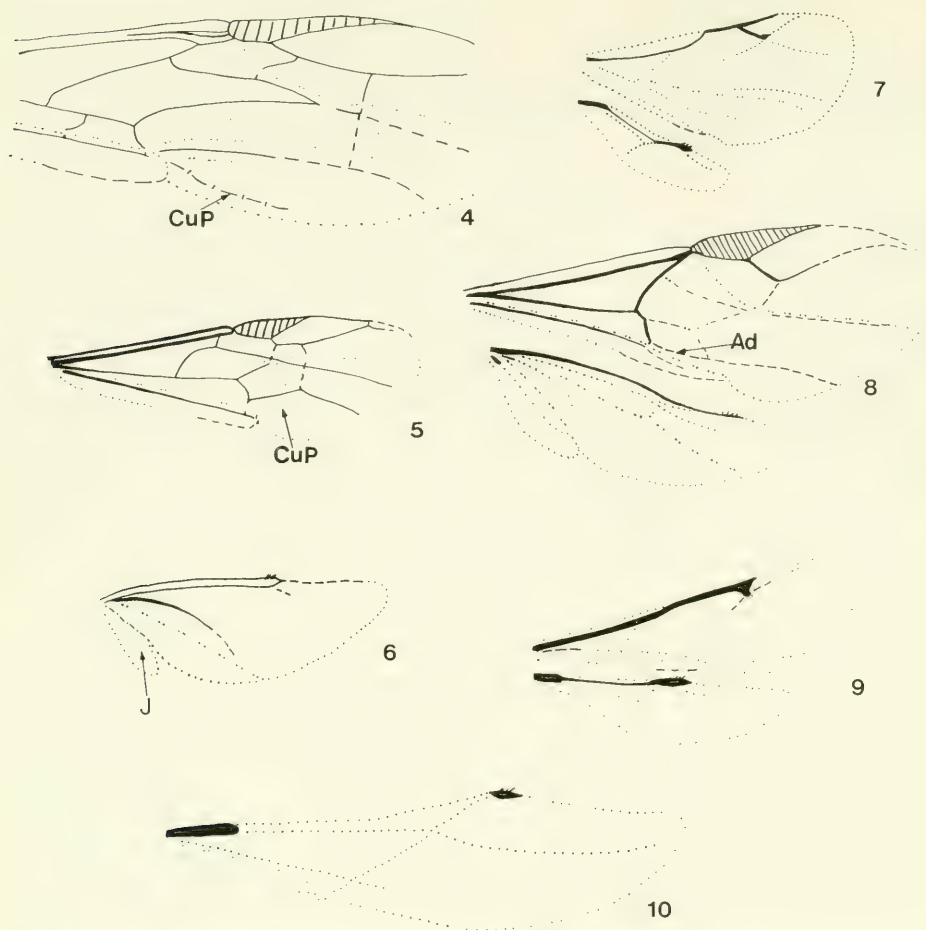


Figs. 1-3. Conventional system for illustrating various features of the Hymenopterous wing. 1, Hypothetical cross section. 2, Large scale figure. 3, Small scale figure. M = margin; Tv = tubular vein; Nv = nebulous vein; Sv = spectral vein; F = flexion line; B = bulla.

3. *Spectral vein* (Figs. 1Sv, 2Sv): an unpigmented vein that is normally invisible by transmitted light but can be seen by light reflected off the wing membrane because its course is marked by a ridge or furrow on the wing surface. If wings are placed in a mounting medium on a slide the spectral veins are usually no longer visible, although nebulous and sclerotized veins are still easily seen. Lines of trichiae on wings are much too variable in occurrence and position to be a reliable guide to the course of spectral veins. The name refers to the transparent, sometimes invisible nature of the veins.

Transitions.—Tubular veins often become nebulous distally or occasionally, if hyaline, they may become spectral. The change is usually abrupt, and the end of the tubular vein often appears sealed by a rounded dark line. Nebulous veins pass gradually into spectral veins, the area of change varying between individuals. The transition is almost never abrupt.

Trace veins.—This term refers indefinitely to what I have called Nebulous and



Figs. 4–10. Samples of wings showing seldom illustrated features, especially spectral veins and flexion lines. 4, Fore wing *Rhopalosoma nearcticum*. 5, Fore wing *Hylaeus ellipticus*. 6, Hind wing *Evania* sp. 7, *Eurytoma* sp. 8, *Deinodryinus atriventris*. 9, *Trimorus* sp. 10, Hind wing *Megaspilus* sp. CuP = postulated distal part of cubitus posterior, a concave vein. J = jugal lobe delimited by a convex folding line. Ad = adventitious vein.

Spectral veins but they are also called Reduced, Evanescent, Atrophied, Relict or Spurious veins. These terms, and others, have been loosely, and often interchangeably used to denote veins that are in the stages of reduction covered by my terms *nebulous* and *spectral*. The term “spurious” is misleading, since it means false, whereas the veins so named are sometimes true though weak veins homologous with normal venation and sometimes not so. The other terms have been so loosely used that they are virtually synonyms. I think it better to use completely new and unambiguously defined terms. The chief trouble with older terms (beside their vagueness) is that it is seldom possible to know whether spectral veins are included, since many illustrators work from wings mounted on slides where the mounting medium and transmitted light most often render the spectral veins invisible. It is also a common practice for taxonomists to treat strongly

colored nebulous veins in the same way as tubular veins while calling weakly pigmented veins by some other term which may, or may not, include spectral veins. The worse practice is to call spectral veins "absent" as part of a 2-term morphocline in which the other term is "present."

OTHER VEIN-LIKE WING FEATURES

Adventitious veins.—These markings appear like nebulous or even tubular veins but occur in places where they cannot be homologized with the normal venation. The name "spurious vein" is sometimes applied but is also used loosely for true spectral veins. Perhaps the best known example is the vertical curved vein anterior to the claval notch in the fore wing of *Helorus*. There is also a frequently seen adventitious vein between M+Cu and 1A in the fore wing of many *Macrocentrus* species. Another example, so far as I know not previously noted, occurs in many Aculeata in the families Dryinidae (Fig. 8Ad), Chrysidae, and Bethyidae. In these the fore wing bears an adventitious vein between Cu-a and Cul but on the opposite side (anterior) of the claval flexion line from 1A. In the first two of these examples the sclerotization is neutral in its dorso-ventral orientation in the membrane but the adventitious vein in Chrysidoidea is convex.

Writers should not call a vein "adventitious" merely because they believe it to be a secondary regeneration of a normal vein (e.g. the vein RS2 in Mutillidae). The apparent homology with a regular vein is clear, even though the phylogenetic history may not be understood.

Flexion lines.—These furrows are defined and discussed by Wootton (1979). They are linear zones of flexibility that seem to govern the changes in airfoil shape during flight. In the Hymenoptera they are, for practical purposes, all concave above, resembling the unpigmented spectral veins but with opposite profile and different function. In wings with dark membranes, however, all the venation, including the spectral veins, is dark but the flexion lines are often much paler, even hyaline. In Hymenoptera with well-developed venations a flexion line immediately anterior to the first anal is a constant feature (here called the claval flexion line [Wootton, 1979]) and it serves as a useful landmark in reduced venations. There are other flexion lines near or between the media and radial sector veins. These are not constant in form or position and are often forked apically. They are generally called medial flexion lines and give well-developed venations of many Hymenoptera a secondary system of flutings apically (Figs. 4, 5).

Bullae.—Where flexion lines cross veins there are short sections of clear, flexible chitin unlike the rest of the veins (Fig. 2B). These areas have received the names Bulla, Fenestra or Thyridial Area but the first name seems most used nowadays. Bullae have been often used as taxonomic characters and their presence or absence should be accurately noted.

CONVENTIONS FOR WING DRAWINGS

To achieve accurate delineation of wing features some standard conventions are needed but standardization in Hymenoptera wing figures is lacking, not only between different authors but even within a single paper. There is a concordance in using continuous double or single lines for tubular veins and one or more kinds of broken lines or stippling for trace veins, sometimes also for flexion lines. The latter are frequently not represented at all and even if indicated there is seldom

more than the claval flexion line drawn. About half the time the same symbol is used for both flexion lines and trace veins, a practice that can lead to serious confusion (Fig. 6). Lastly, wing margins are usually drawn as a single continuous line, a convention that can at times make it impossible to interpret the presence or length of the costal vein, a character of considerable taxonomic use.

A drawing of a wing should have the following features:

1. Parts of the margin with and without a marginal vein should be distinguishable (Figs. 2, 7, 9, 10).

2. Three stages of vein reduction, tubular, nebulous and spectral, should be represented by different symbols that also depict obviously, the differing degrees of visibility. I think it important to distinguish nebulous from spectral veins because different lighting techniques are required to see them. On the veins bullae should be indicated.

3. Flexion lines should be represented by a symbol different from those used for veins.

4. An option should be, when needed, special symbols for such occasionally important features as the convex jugal fold (Fig. 6), concave veins (Figs. 4, 5) and adventitious veins (Fig. 8).

The above requirements come closest to being met by the scheme adopted by Richards (1956) whose conventions sometimes fail to distinguish nebulous from spectral veins. The conventions used by Evans (1978) are almost as good but the symbolization is not consistent within the paper. Neither Richards nor Evans explain their symbols for veins and flexion lines and both have inconsistencies among their figures. Quite recently Day (1984) introduced a new system for naming wing features but did not explain the symbolization in his figures. I find his definitions of various stages of vein reduction too indefinite to adopt for practical use and in addition, he groups both nebular and spectral veins under the term "relict." The latter grouping is defensible but I prefer to keep the two distinct for reasons discussed above. Other works on Hymenoptera have many imperfections in symbolizations and most authors appear not to have given serious consideration to accurate depiction of all wing features or, even less desirable, to have left it entirely in the hands of an artist.

The system I propose is closest to that of Richards (1956) but has some improvements. Tubular veins are indicated by continuous lines: nebular veins by dashed lines: spectral veins by dotted lines. All the vein symbols may be used singly or doubly depending on the size of the figure and width of the vein; furthermore the tubular and nebulous vein symbols may, if doubled, be filled by stippling to indicate degree of pigmentation should it be desirable (Fig. 2). Concave flexion lines are represented by tandem paired dots, i.e. a dotted line with every 3rd dot missing or an alternating pattern of 2 dots present, 2 missing. For the convex jugal fold I suggest a line of alternating dots and dashes (Fig. 6). Wing edges, which should not be confused with spectral veins, can be represented by a dotted line if veinless, solid or dashed line if occupied by a tubular or a nebulous vein. If confusion between spectral veins and wing margins is feared, then smaller and more closely spaced dots could be used for veinless margins or hairs could be added. Special, but different symbols should be used for seldom seen features such as adventitious veins (Fig. 8) or concave veins (Figs. 4, 5).

CONCLUSIONS

Careful observation and careful description of trace venation and flexion lines will result in keys that are much easier to use accurately. In phylogenetic studies, trace venation can help settle questions of relationships. More important, perhaps, taxonomic characters can be found also in the course of flexion lines. It should be recalled that bullae, which are traditional taxonomic characters, mark where flexion lines cross veins so their presence is correlated and can be helpful in tracing weak flexion lines. Finally one should remember that concavity or convexity of veins and flexion lines is reversed when they are observed from the underside of the wing.

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A NEW SPECIES OF *RIGGIELLA* KORMILEV FROM MEXICO
(HEMIPTERA: LYGAEIDAE: BLISSINAE)

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Abstract. — *Riggiella lucida* is described as a new species from southern Mexico. The bamboo *Chusquea* sp. is established as the breeding host. *Riggiella lucida* is the first species of *Riggiella* known from north of South America. The third, fourth and fifth instar nymphs are described. The phylogenetic relationships of *Riggiella* are reevaluated. A dorsal view of the holotype is included.

The genus *Riggiella* Kormilev contains some of the largest and the most extremely flattened species of New World Blissinae.

Previously three species have been described, all from South America. The present paper describes the first species from Central America and establishes bamboos as definite host plants. The availability of nymphs enables the phylogenetic relationships of the genus to be more adequately understood.

Phylogenetic relationships: Slater (1979) was somewhat ambiguous concerning the phylogenetic position of *Riggiella*. His cladogram (p. 31) placed it in a clade containing a number of Old World taxa (and also *Patritius* Distant from the Western Hemisphere) on the basis of the derived feature of multispinose forefemora. Slater (1979: 34) recognized the possibility of homoplasy in this character. On page 43 he suggests the possibility of the Oriental genus *Scansidemus* Slater and Wilcox being the sister taxon of *Riggiella*.

The availability of nymphs seems to clearly indicate that Slater's conclusions regarding the relationships of *Riggiella* were wrong. The large elliptical SGA (see Slater [1979] for explanation of abbreviations) sclerotized plates of the nymph constitute an important synapomorphy that allies *Riggiella* with the Western Hemisphere genus *Toonglasa* Distant and a series of Madagascar and Ethiopian genera (including *Ramadademus* Slater from Madagascar the species of which also have a broad flattened body and multispinose forefemora).

In the Western Hemisphere the sister group to *Riggiella* would thus appear to be *Toonglasa*, many species of which now are known to breed on bamboos. Nymphs of *Riggiella lucida* will key to *Toonglasa* (= *Extarademus* Slater and Wilcox) in Slater (1979).

All measurements are in millimeters.

Riggiella lucida NEW SPECIES

Fig. 1

Adult.—General coloration black. Apex of tylus, femora, proximal and distal ends of tibiae, tarsi, labium, lateral margins of abdomen, and raised cubital vein of clavus yellow. Hemelytra strongly contrasting black and almost white, the light coloration as follows: clavus laterad of cubital vein, entire corium mesad of corial furrow from base to slightly beyond distal end of claval commissure (except for a row of dark punctures along outer margin of medius and a dark suffused area midway along region between medius and corial furrow); broad lateral margins of membrane from middle of apical corial margin caudad. Smooth posterior portion of pronotum mahogany brown, first antennal segment yellowish-brown, segment two dark brown but contrasting with black third and fourth segments.

Head and pronotum shining dorsally. Scutellum with pruinosity confined to a narrow basal stripe. Clavus, corium and membrane dull except for a strongly contrasting shining stripe occupying all of corium laterad of corial furrow, becoming broadened and lobate posteriorly and terminating near middle of corium at level of middle of apical corial margin. Head pruinose ventrally behind eyes, but subshining mesally. Propleuron and sternum pruinose behind acetabula but shining anteriorly except for a pruinose stripe extending from meson immediately in front of forecoxae diagonally forward to end at anterior margin of thorax midway between meson and lateral margin, and narrowing anteriorly.

General shape of body and position of punctures typical for genus, but body somewhat less broadened than in other species. Head below lacking a pair of genal tusks, but strongly produced as a large swollen rugose "carina" mesally. Spine at distal end of foretibia reduced to a short tubercle. A short blunt tubercle present near inner proximal end of each foretibia. Forefemur below with a large broadened bifid distal spine and five elongate sharp, distally curving, and evenly spaced spines proximally.

Length head 0.68, width 0.96; interocular space 0.64. Length pronotum 1.44, width 2.02. Length scutellum 0.94, width 1.18. Length claval commissure 0.70. Midline distance apex clavus–apex corium 1.60; midline distance apex corium–apex abdomen 2.24. Length labial segments I 0.30, II 0.20, III 0.24, IV 0.24. Length antennal segments I 0.24, II 0.68, III 0.72, IV 0.92. Total body length 7.52.

Holotype: ♂. MEXICO: *Chiapas*: Finca Prusia Queretaro. 24.I.1985 (H. Velasco). In Instituto de Biología, Universidad Nacional Autónoma de México, México D.F.

Paratypes: MEXICO: 1 ♂, 3 ♀ same locality as holotype. (1 ♀ label identical with that of holotype; 1 ♂ lacking "Queretaro" and with H. Garcia as collector; 1 ♀ lacking "Queretaro" and with M. Vertiz as collector; 1 ♀ data as for holotype but F. Arias collector.) In Instituto de Biología, Universidad Nacional Autónoma de México, México D.F., and J. A. Slater collections.

Adults of *Riggiella lucida* will key with some difficulty to *Riggiella vianai* Kormilev in Slater (1979). Within the genus *Riggiella*, *lucida* is not particularly similar to *vianai* or to either of the other two species of *Riggiella* (*distinctus* and *planus* Slater and Ahmad).

Riggiella lucida is a much less broadened species than any of those previously



Fig. 1. *Riggiella lucida* New Species. Dorsal view.

described. In the other three species the pronotum is approximately twice as wide as the median length whereas in *lucida* it is only slightly more than 1½ times as wide. This gives *lucida* somewhat the appearance of some species of *Patritius*. However, the strongly flattened body and particularly the shape of the metathoracic scent gland auricle clearly demonstrate that *lucida* is congeneric with the other species of *Riggiella*.

In addition to the less strongly broadened body shape *lucida* may readily be distinguished by the loss of pruinosity laterally on the scutellum, the lack of a dark stripe on the corium immediately adjacent to the claval suture and the lack of short tuberculate projections on the genae.

This latter feature is interesting as the mesal surface of the head below is produced into a swollen lobe that is strongly suggestive of a fusion of the genal "tusks" of the other species. This presumably apomorphic condition taken together with the apomorphic condition of reduced pruinosity on the scutellum, pronotum, propleuron and head suggests that the less broadened body form may be secondarily derived from the more broadened South American species rather than the reverse.

The presence of a species of *Riggiella* as far north as southern Mexico is another example of the close relationship of so many of the Central and South American blissine taxa.

IMMATURE STAGES OF *RIGGIELLA LUCIDA*

Fifth instar nymph: MEXICO: (*Chiapas*: Finca Prusia Queretaro).—Body shape moderately broadened and robust as in adult. Head, pronotum, distal portion of scutellum, most of mesothoracic wing pads and legs bright yellow. Distal ends of wing pads strongly contrasting dark brown and scutellum extensively suffused with dark brown. First antennal segment dull yellow, segments two and three dark brown, segment four black. Central area of tibiae and second tarsal segment pale brown. Abdominal terga 2-3-4-5 posteriorly and mesally broadly banded with rose-pink, strongly contrasting with white coloration of remainder of abdomen. No TM sclerites present anterior to TM 7, sclerites of TML row small, ovoid. No TL 2-5 sclerites, TL 6 minute, elongate. TL 7 distinctly separated from TM 7, the anterior of the latter sinuate, produced mesally. TML 7 and TMA 7 fused. SGA 4-5 much larger than SGP 4-5 and forming a large half-circular sclerite but smaller than SGA 5-6 which is not only broader but conical or almost pyramidal in shape. Dorsal abdominal sclerites pale brown except for TM 7, 8, and 9 which are a strongly contrasting chocolate brown color.

No SM 4 or 5 sclerites. SM 6 well developed and triangular, SM 7 broadly rounded almost attaining anterior margin of sternum 7. SML 7 sclerites very large and lobate with smaller but distinct and similarly shaped sclerites on sterna five and six. These sclerites suggest that Slater (1979) is incorrect in believing that what he labels as SML 7 is serially homologous with his SML row for such a row is present in this insect in addition to the sclerites noted here.

Length head 0.54, width 0.88; interocular space 0.62. Length pronotum 0.94, width 1.70. Length mesothoracic wing pads 1.88. Length abdomen 2.96. Length labial segments I 0.20, II 0.24, III 0.22, IV 0.20. Length antennal segments I 0.16, II 0.58, III 0.44, IV 0.70. Total body length 5.84.

Fourth instar nymph: Same locality.—Similar to instar 5, but with scutellar

area completely dark brown. Length head 0.48, width 0.68; interocular space 0.44. Length pronotum 0.64, width 1.14. Length mesothoracic wing pads 0.86. Length abdomen 2.76. Length labial segments I 0.20, II 0.20, III 0.18, IV 0.20. Length antennal segments I 0.14, II 0.32, III 0.36, IV 0.56. Total body length 5.12.

Third instar nymph: Same locality.—Similar to preceding. Length head 0.44, width 0.56; interocular space 0.42. Length pronotum 0.44, width 0.96. Length mesothoracic wing pads 0.38. Length abdomen 1.88. Length labial segments I 0.18, II 0.14, III 0.16, IV 0.16. Length antennal segments I 0.10, II 0.24, III 0.26, IV 0.42. Total body length 3.60.

Biology.—The type locality of *Riggiella lucida* is near the Guatemalan border. This is a tropical area. Adults and nymphs were taken on a bamboo (*Chusquea* sp.), the nymphs and one male being taken on the leaves, the other adults behind the sheaths. Kormilev (1949) reported *Riggiella vianai* as taken on bamboo. However, the present record is the first that definitely establishes a breeding population for a species of *Riggiella* on bamboo.

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OBSERVATIONS ON THE NESTING BEHAVIORS OF
TACHYTES PARVUS FOX AND *T. OBDUCTUS* FOX
(HYMENOPTERA: SPHECIDAE)

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Abstract.—Various components of the nesting behavior of 11 females of *Tachytes parvus* Fox were studied in upstate New York during July and August 1984. Similar observations on two females of *T. obductus* Fox nesting at the same locality later in the year are included. Particular attention is paid to nest initiation, burrow construction, prey capture and transport, nest entry and exit, cleptoparasitism by miltogrammine flies, wasp countermaneuvers, nest architecture and dimensions, and cell contents, including prey, immature wasps and egg placement. Detailed comparisons are made between the nesting components of the two species based upon this study and review of the literature.

The genus *Tachytes* contains mostly stout-bodied, hairy, beelike wasps distributed throughout the temperate and tropical regions of the world. Bohart and Menke (1976) list 28 nearctic species belonging to several species groups. Members of the *aurulentus* group provision their nests with Tettigoniidae and some of the species have been rather well studied (see Evans and Kurczewski, 1966; Kurczewski and Ginsburg, 1971). Prey records for species belonging to the *pepticus* and *distinctus* groups comprise Acrididae; some of these species have been studied sparingly (see Williams, 1913; Evans and Kurczewski, 1966). Members of the *mergus* group, including *T. mergus* Fox, have a number of unique morphological and behavioral characteristics, which include preying upon Tridactylidae (Krombein and Kurczewski, 1963; Kurczewski, 1966). Behaviorally, the *abdominalis* group contains the most heterogeneous assemblage of species of *Tachytes* in the nearctic region. *T. intermedius* (Viereck) stores Tridactylidae but its behavior differs considerably from that of *T. mergus* (see Kurczewski, 1966; Kurczewski and Kurczewski, 1984). *T. chrysopyga* (Spinola) stores Acrididae, *T. abdominalis* (Say) uses both Acrididae and Tetrigidae, and *T. obductus* Fox preys upon Tetrigidae (Williams, 1913; Kurczewski and Kurczewski, 1971; Kurczewski, 1976).

Tachytes parvus Fox (= *T. pattoni* Banks), another member of the *abdominalis* group, also stores Tetrigidae based upon a single record (Kurczewski and Kurczewski, 1971). Otherwise, nothing is known about the ecology or behavior of this species. It occurs from New Jersey to Florida, westward into Idaho and California (Krombein, 1979).

We found *T. parvus* nesting in a sand-gravel ridge in the town of Sennett, 3.2 km east of Auburn, Cayuga County, NY—400 km outside of its known range—

from 23 July to 8 August 1984. Judging from the contents of nests we excavated the species had been nesting at this site since 18 July. We observed males pursuing females in an attempt to mate with them during 23–28 July, but thereafter no males were seen. We unearthed two females on 28 July from an old (1983?) nest: a teneral wasp inside of its cocoon; and, another wasp near a broken cocoon beginning to dig its way upward through the soil. This indicates that a portion of the 1984 population had yet to emerge.

We located 11 nests of *T. parvus* between 23 July and 1 August 1984. Nine of the nests were situated in moist, moderately vegetated sand and gravel toward the bottom of the ridge (Fig. 1), and two of the nests were located upslope in almost bare sand. The nest entrances were concealed either at the bases of clumps of grasses, underneath overhanging stems or leaves, between sizeable pebbles, or in a dog footprint (Fig. 2). During provisioning the entrances were left open, but during the construction of a new cell or, sometimes, during the night, the openings were plugged with sand or fine gravel.

Females beginning new nests were observed walking slowly on the sand in a zigzag manner, pausing under leaves, decumbent stems or in depressions, and sampling the sand with the mandibles. Such females also looked into holes, 4–6 mm in diameter, entered partly, then backed out and walked elsewhere. One female searched for a place to dig between 1350 and 1430 h (EDT) on 29 July at a sand surface temperature of 35°C and air (shade) temperature of 29°C. Another female was seen to enter a shallow depression on 23 July and loosen sand with the mandibles. She removed this soil backward with the forelegs and distributed the sand circularly around the rim of the entrance with the hindlegs and abdominal apex, always keeping the midlegs anchored against the sides of the opening. Within 3 min this wasp had disappeared from sight, the only evidence of burrow construction being damp sand pushed periodically into the entrance. After 134 min of (apparent) burrow construction the female appeared in the entrance headfirst, paused, looked around and then made a 4.5 min-long hovering flight (orientation?) above the area of the entrance. During the initial 2 min of the flight, the wasp vigorously wagged her body from side to side while mostly facing the entrance at a height of 20–40 cm. She proceeded to elevate her flight to 1 m or slightly higher during the next 1.5 min, still wagging her body while facing the entrance. She continued to fly higher and further from the entrance during the next min and then disappeared from sight. The flight took place at a sand surface temperature of 52°C and air (shade) temperature of 38°C.

Several females were observed capturing nymphal *Tetrix o. ornata* (Say) (Tetrigidae) on damp sand amidst moderately dense vegetation, often only 1–5 m from their nest entrances. Such wasps searched for prey by flying slowly and sinuously, sometimes hovering, 15–30 cm above the sand. They pounced upon their prey by flying rapidly downward, landed atop the dorsum, bent the abdominal apex underneath the prey's thorax and inserted the sting for a few s. The wasp then remained motionless or cleaned herself for 5–6 s, grasped the prey, usually ventral side upward, by its antennae and body with the mandibles and legs, respectively, and flew rapidly toward the nest. In the vicinity of the nest entrance the provisioning female assumed a slow wagging flight. Smaller, immature prey were difficult to discern beneath the wasps but two larger, adult prey



Figs. 1, 2. 1, Nesting habitat of *Tachytes parvus*, 3.2 km east of Auburn, Cayuga County, New York. Nine nests were located in the moderately vegetated, moist sand and gravel in the foreground. 2, Entrance to nest of *Tachytes parvus*, with marking stake located 2 cm to right. Note sparse vegetation and absence of tumulus.

protruded well beyond the tip of the wasps' abdomens during flight and upon landing.

Provisioning females brought successive prey to their entrances between 1151 and 1659 h at intervals of 1–32 ($\bar{x}$ = 5.5, N = 28) min. There were no significant differences between the mean provisioning rates of five females. A provisioning wasp flew slowly, ca. 30–40 cm above the sand, in an extensive wagglng flight, sometimes lasting 30–60 s, then reduced the height of the flight to ca. 20 cm prior to entering the open nest. Some wasps landed up to 60–70 cm from their entrances and paused on the sand for 30–60 s prior to entry, whereas females pursued by cleptoparasitic Miltogramminae (Diptera: Sarcophagidae) did not enter but turned abruptly and flew away only to return s or min later. After entering with prey the females spent from 0.3 to 2.0 ($\bar{x}$ = 1.1, N = 22) min inside the nest before exiting headfirst. Most wasps exited rapidly in flight but a few spent 5–50 s in a low, wagglng flight (reorientation?) above the area of the entrance prior to flying away. Entry flights of non-provisioning females were straight and faster than those of provisioning wasps.

When attempting to elude species of Miltogramminae, the wasps exhibited atypical flight patterns and spent several min per provisioning trip. Sometimes the wagglng flight of the provisioning female sufficed as a distractor, but four times a female of *Phrosinella aurifacies* Downes and three times one of *Senotainia trilineata* (Wulp) entered an entrance shortly after the provisioning wasp had gone inside. The flies exited 5–8 s later. Twice, females with prey were seen to convert their wagglng provisioning flight into a rapid straight flight several meters in length in an attempt to elude a trailing *S. trilineata*. Both times the provisioning wasp's quick flight was successful and she returned and entered the nest minus the fly. But one wasp with an adult prey returned and landed with an *S. vigilans* Allen female riding on the prey's protruding abdominal sternites. The *S. vigilans* had been seen earlier lurking on upright vegetation near the wasp's entrance.

Provisioning wasps pursued by miltogrammine flies also landed 30–90 cm from the entrance, often in the shade beneath vegetation, and remained still, interspersed with wagglng flights and rapid "escape" flights. One such female spent 8 min attempting unsuccessfully to evade two trailing *S. trilineata* females. If unsuccessful in eluding an *S. trilineata* in the vicinity of their nest, some provisioning wasps flew at, "buted" (see Lin, 1963) and knocked the fly to the ground. Another *S. trilineata*, which had sat on an overhanging stem near a wasp's entrance, was actually attacked by the provisioning wasp in midair, knocked to the ground and stung, after the female had released her prey. The fly lay immobile for 1.5 min after which it was placed in a vial and began to recover from the effects of the sting. The wasp flew away, abandoning its prey on the sand. Prior to this attack the provisioning wasp and fly had "faced-off" (see Spofford et al., 1986) on the sand for 8 s. The same wasp, upon returning with an additional prey, was pursued in flight by another *S. trilineata*, which then attached itself by clinging to the pair and attempted to larviposit on the prey. The wasp landed, cleaned herself, groomed the prey for 8 s, restung it and flew into the entrance. The female met the same fate on her next provisioning flight and she reacted in the same manner, only this time she turned, after exiting, and reentered her nest instead of flying away rapidly. Whether or not reentry was related to the attempted larviposition by the fly is unknown. Despite all of the various behavioral mech-

anisms exhibited by this species of wasp in an attempt to deter cleptoparasitic flies of the tribe Miltogrammini from larvipositing on the prey, 2 of 19 (10.5%) of the cells when examined contained maggots rather than wasp eggs or larvae. Both maggots formed puparia from which male *S. trilineata* and *P. aurifacies* emerged on 13 August 1984 and 24 April 1985, respectively.

Four females of *T. parvus* spent 50, 53, 75 and 80 min constructing an additional cell inside the nest beginning at 1411, 1537, 1338, and 1132 h, respectively. During this addition the wasp must have removed sand from the new excavation to an old (side) burrow because she did not bring sand out of the entrance onto the surface. The tumulus thus becomes nonexistent after the construction of the main burrow and first cell.

We excavated five unfinished nests of this species, the largest one containing eight fully-provisioned cells. Four of the five nests were contained within an area with a radius of 1.2 m. Entrances to newly constructed nests ($N = 4$) were 4–5 mm in diam and were surrounded by circular tumuli, ca. 2.5 cm in diam, or fronted by fan-shaped tumuli measuring ca. $3.5\text{--}4.0 \times 4.0\text{--}4.5$ cm. In a day or so these tumuli become sun-dried and windblown and are virtually indistinguishable from the surrounding sand. Older nests actually have 5–10-mm-long, fan-shaped “runways” leading into their entrances. The burrows entered the sand at $25^{\circ}\text{--}45^{\circ}$ angles to the surface for 3–6 cm, then either looped backwards or went almost vertically; some even turned or looped a second time (Fig. 3). One such burrow, 22.7 cm long, was traced to its blind ending at a depth of 8.8 cm beneath the surface, and another, 15.5 cm long, to a cell. Four of the five nests had blind chambers (spurs), 1.5–2.1 cm long; three were just beneath the entrance and one, at a depth of 3.8 cm. Cells containing prey and wasps in various stages of development were unearthed either below the entrance amidst a myriad of small pebbles and rootlets or, more usually, spaced widely in various directions in bare sand, 9–59 cm from the entrance (Fig. 3). In four of the five nests the cells were unearthed uphill of the entrance, the exception being a nest on top of the ridge in bare, dry, loose sand. Adjacent cells in one nest were uncovered 1–14 ($\bar{x} = 5.4$; $N = 7$) cm apart.

The cells were found at various depths, depending upon the type of soil, amounts of moisture and vegetation (rootlets), and slope of sand surface. For example, one cell in highly vegetated, moist, gravelly soil was only 7.7 cm deep, including cell height; six cells in moderately vegetated, moist, gravelly-sand, 8.0–10.5 cm deep; nine cells in sparsely vegetated, moderately moist, coarse sand, 11.0–12.0 cm deep; eight cells in almost bare, drier sand, 12.5–15.0 cm deep; and, four cells in bare, dry, loose sand, 15.5–16.0 cm deep. In one nest the oldest cells, as based upon their contents, were located furthest from the entrance at increasingly greater depths. Another nest had all but two of eight cells at about the same depth, but again the cells furthest from the entrance were invariably the oldest.

The cells were either perfectly ovoidal or slightly narrower at their distal ends. They ranged in size from 5×10 to 7×14 ($\bar{x} = 6.0 \times 12.3$; $N = 11$) mm in height and length, respectively. Although eight smaller cells ($5\text{--}6 \times 10\text{--}12$ mm) each contained only 4, 5 or 6 prey and eight larger ones ($6\text{--}7 \times 13\text{--}14$ mm) each held 7, 8 or 9 prey, suggesting a correlation between cell size and number of prey per cell, the smaller cells were unearthed in moderately vegetated, moist, gravelly-sand and the larger cells in almost bare, drier sand.

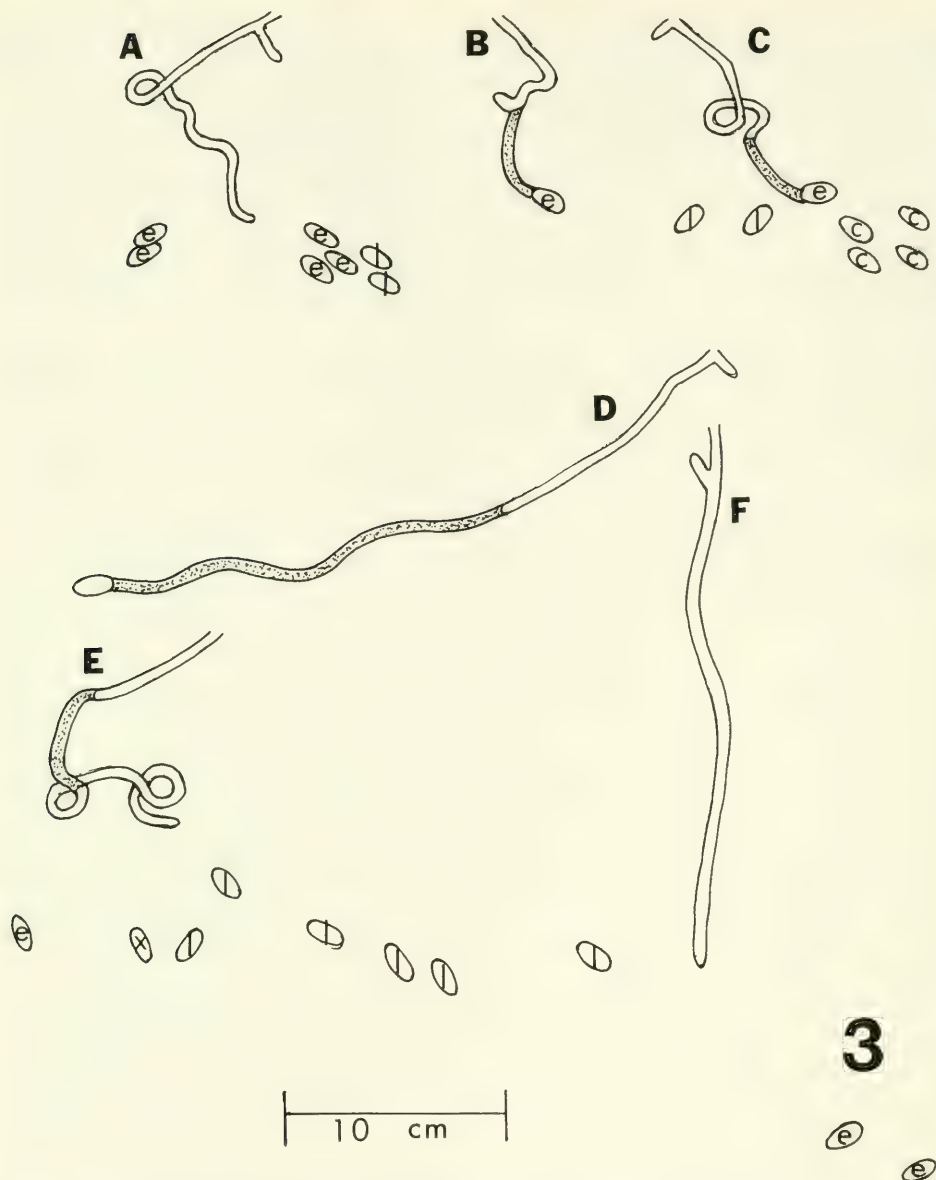


Fig. 3. Nests of *Tachytes parvus* (A-E) and *T. obductus* (F), as viewed from the side, showing burrows and cells. Nest E is 8-celled and nest F, 2-celled. Cell contents are as follows: e, egg; l, larva; c, cocoon; x, maggots. Stippling indicates burrow is filled with sand. The scale refers to all nests except nest E in which the cell distances have been compacted horizontally.

A total of 99 nymphal and 3 adult prey were recovered from the cells and 24 of these were identified as *Tetrax o. ornata*. The number of prey stored in a cell varied from 4 to 9 ($\bar{x} = 6.0$; $N = 17$), although, as indicated, cells within a nest tended to contain similar numbers of prey per cell. Individual prey weighed (wet) from 3.0 to 29.3 ($\bar{x} = 13.8$; $N = 89$) mg, whereas the total weight of all prey in a

cell ranged from 46 to 141 ($\bar{x}$ = 88.4; N = 14) mg. Cells with more prey almost invariably contained more biomass than cells with fewer prey. Three female wasps weighed (wet) 27, 39, and 39 mg.

The prey were positioned in the cells variously: 48, head inward and ventral side upward; 6, head outward and ventral side upward; 10, head inward and dorsal side upward; 6, head inward and on the side; and, 1, head outward and on the side. Eggs (8) or small larvae (3) were attached to prey that were positioned head inward and ventral side upward, usually near the top of the cell atop other prey.

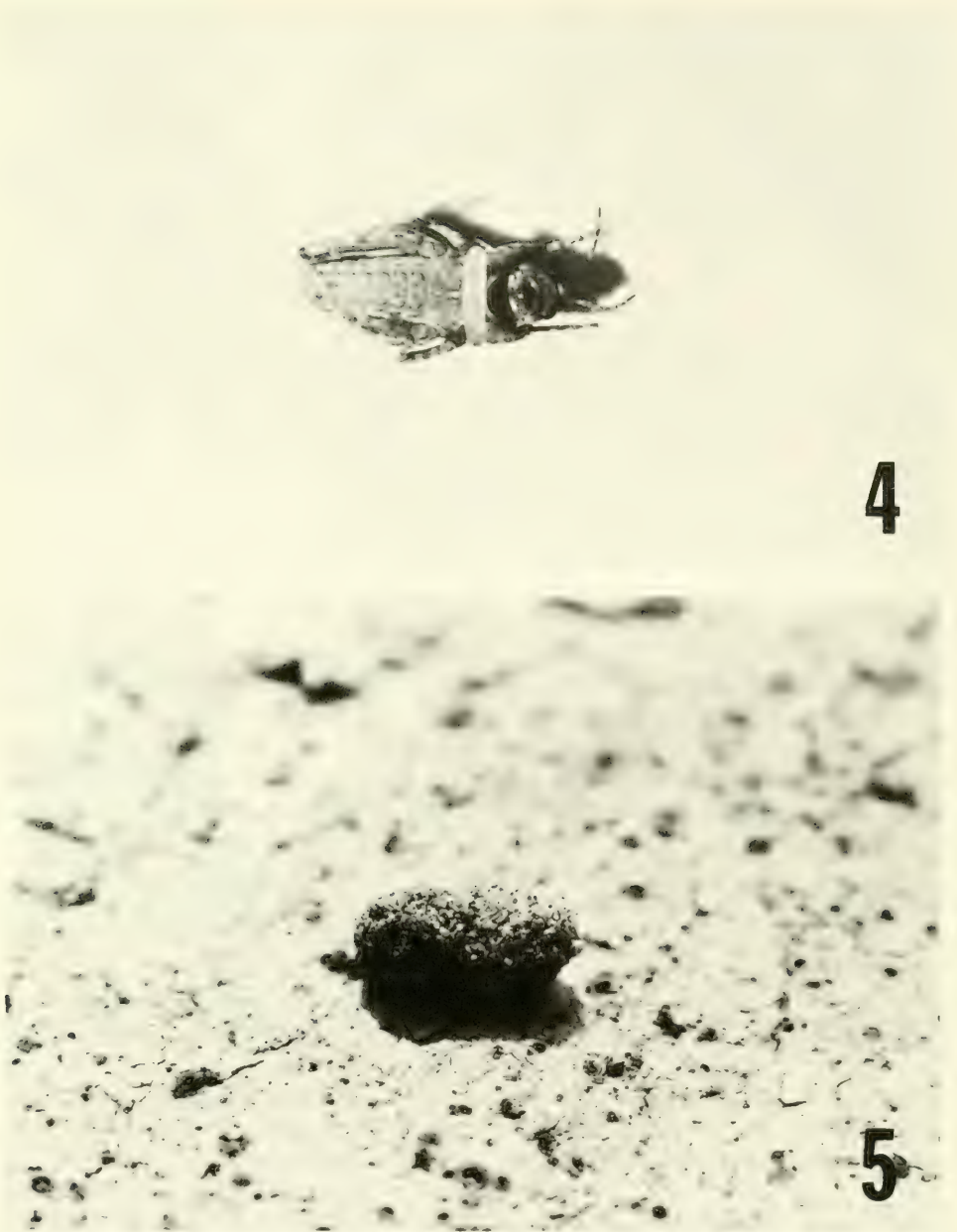
The egg of *T. parvus* is white and sausage-shaped and is affixed by its cephalic end to a forecoxal corium of the prey, extending transversely between the first two pairs of legs (Fig. 4). Of eight eggs attached to prey, five were affixed to the right forecoxal corium and three to the left. Two eggs were placed on the third largest prey in the cell and one on the second largest. Larvae hatched in ca. 48 h. Mature larvae began spinning cocoons ca. 5 d later. The cocoon is ovoidal and consists of silk, saliva and sand grains (Fig. 5). Four cocoons ranged in size from 3.0×7.0 to 3.5×8.0 ($\bar{x}$ = 3.3×7.6) mm.

At the same site later in the year (26–31 Aug 1984) we located two females of *T. obductus* nesting in the top and in the upper slope of the sand-gravel ridge in which *T. parvus* had nested. The first female had a nest in bare sand topped with a gravelly crust. Her burrow, 7 mm in diameter, with a small side chamber (spur), 2 cm down, went almost vertically downward for 24 cm. There was no tumulus on the sand surface. Two cells were located at depths of 33 and 34 cm, including cell height, 10 and 15 cm southwest of the burrow terminus. Cell A was 6×14 mm in height and length, respectively, and contained four immature *Tetrix o. ornata*. Three of the tetrigids were positioned head inward and ventral side upward, including the egg-bearer, and one, head inward and dorsal side upward. The egg was attached to the right forecoxal corium of a medium-sized prey (wet wt., 22 mg), and it extended transversely between the fore- and midcoxae. The total weight (wet) of all prey in the cell was 96 mg, with individual prey weights ranging from 11.5 to 31.0 mg.

Cell B contained five *T. o. ornata*, including four immatures and one adult male. Two of these prey, including the egg-bearer at the top of the cell, were positioned head inward and ventral side upward and one, head inward and dorsal side upward. The cell measured 7×13 mm in height and length, respectively. The egg was attached to the right forecoxal corium of an immature tetrigid, as described above. The egg-bearing prey weighed (wet) 21 mg, and the adult male, 27 mg. The total weight of all prey in the cell was 106 mg.

The burrow of the second female, 6 mm in diameter, entered the sandy cliff perpendicularly, and then turned and proceeded almost straight downward. The tumulus, 8.5×14.5 cm, consisting of freshly removed, agglutinated pellets of damp sand, laid below the entrance. We spent parts of three days in excavating this nest but were unsuccessful in finding any of the cells. Based upon the sequence of provisioning, including the intermittent lengthy pauses, we believe there were two cells each containing four prey. We observed this female, one day before she began provisioning, entering open holes in the cliff face, presumably searching for a place to begin digging.

Females of *T. obductus* were observed hunting for prey in low quick flights, interspersed with searching under *Equisetum* and other low plants within 1.1–



Figs. 4, 5. 4, Egg of *Tachytes parvus* affixed transversely to immature *Tetrix o. ornata* between first two pairs of legs. 5, Cocoon of *Tachytes parvus* consisting of sand grains, silk and saliva.

4.0 m of their nest entrances. The provisioning wasps were observed arriving from distances of 50–70 cm in rapid, sinuous flights, 10 cm or less above the sand surface, and quickly plunging into their open entrances, holding the prey underneath. One provisioning wasp landed 30 cm from her entrance, rested atop her prey, and then flew into the entrance. Twice, female *A* was pursued into her entrance by a female of *Senotainia vigilans*, but neither cell was found to be

cleptoparasitized when this nest was excavated. After placing prey in their nests the wasps exited in rapid flights, less than 50 cm above the sand surface, except for one female which turned and hovered, facing the entrance, for 20 s before flying away. Once, female *B* appeared headfirst in her entrance, after taking in prey, came out five times to obtain sand, each time backing in with a load, then turned around and plugged the opening with sand. The two wasps spent 47 and 54 min, respectively, apparently to construct an additional cell. They utilized from 2 to 23 ($\bar{x}$ = 9.4; N = 12) min between successive provisioning trips between 1335 to 1458 h (EDT). The wasps stayed inside from 0.8 to 2.5 ($\bar{x}$ = 1.6; N = 12) min between entering with prey and exiting from the entrance.

DISCUSSION

Tachytes obductus and *T. parvus*, both members of the *abdominalis* group, are rather similar in size, adult external morphology, geographical distribution, habitat, nesting behavior and prey preference. Both are "small" species of *Tachytes*, the females averaging ca. 10 mm in body length. *T. obductus* averages slightly larger than *T. parvus*, but there is size overlap. As members of the *abdominalis* group, *T. obductus* and *T. parvus* share a number of external adult morphological characteristics (Banks, 1942). However, in the field, the two species are recognized easily because *T. obductus* is all-black while in *T. parvus* the first two or three abdominal segments are rufous. The species' ranges are sympatric throughout much of the eastern United States east of the 100th meridian, with *T. parvus* extending westward into Idaho and California (Krombein, 1979). We have found both *T. obductus* and *T. parvus* nesting in the same area of sand-gravel, constructing nests of similar architecture and dimensions, and preying upon the same species of Tetrigidae.

Although the two species may occupy the same area of friable soil *T. obductus* prefers bare, dry slopes and hills of sand-gravel, whereas *T. parvus* prefers moderately vegetated, rather flat, moist sand-gravel. Kurczewski and Kurczewski (1971) also noted *T. obductus* nesting in the slope and on the flats of a sand-gravel "bank." The area where F. E. Kurczewski (1976) observed this species nesting near Sennett, New York is a mixed, coarse sand and fine gravel slope. Kurczewski and Kurczewski (1971) reported *T. parvus* (= *T. pattoni*) flying with prey at Kill Devil Hills, North Carolina. This area comprised moderately vegetated, moist sand flats behind the beach. In central New York where the present studies were made, *T. parvus* nested earlier (18 July–8 August) than *T. obductus* (14 August–1 September). Kurczewski and Kurczewski (1971) reported the latter species nesting from 29 July to 10 August in Albany County, New York. One female of *T. parvus* in the CESF Insect Museum was collected on 10 June 1983 (Albany Co., New York; J. C. Allen), further indicating that this species may nest earlier than *T. obductus*.

In searching for a place to nest the two species exhibit similar behavior. They fly slowly, periodically land and examine, and, sometimes enter, open holes and depressions, and, occasionally, dig with the mandibles. Although initial burrow construction was observed only for *T. parvus*, the components exhibited while building additional cells are similar for the two species, both taking approximately one hour to add a cell to a nest, usually during early-mid afternoon. Tumuli of *T. obductus* nests in slopes are distinctly ovoidal, whereas those of *T. parvus* nests in flat sand are slightly ovoidal or circular. In both species the tumulus becomes

obsolete due to the action of the sun and wind. In both *T. obductus* and *T. parvus* the entrance remains open during provisioning, but may be plugged during the addition of a new cell or during the night (*T. parvus*). Both *T. obductus* and *T. parvus* hunt for prey in late morning and throughout much of the afternoon, pausing only to feed and construct additional cells. *T. obductus* searches for prey 1–4 m from its nest in low, rapid flights, whereas *T. parvus* hunts 1–5 m from the entrance in slow, sinuous, sometimes hovering, flights. Williams (1913) noted *T. abdominalis* (Say), a species similar to *T. parvus*, hunting “rather slowly,” but he reported *T. obductus* running on the ground, while hunting, “at a moderate speed . . .” Components of prey capture appear to be essentially identical in *T. obductus* and *T. parvus*. Prey transport in the two species differs strikingly, however, and may be correlated with the prey searching flights. Provisioning females of *T. obductus* return to the nest in rapid, sinuous flights, 10 cm or less above the ground, and plunge quickly into their entrances, whereas females of *T. parvus* with prey exhibit a slow, wagging flight, 20–40 cm above the entrance, prior to entry. In the present study females of *T. obductus* spent about twice as much time in obtaining prey as did females of *T. parvus*, and about 1.5 times as long between entering with prey and exiting. These durations may reflect the abundance of prey at different times of the season and the differential depths of the cells, respectively. Both species exit in a rather straight, rapid flight.

We found no evidence of cleptoparasitism by miltogrammine flies (Sarcophagidae) in our examination of the cells of *T. obductus*, nor has any such cleptoparasitism been reported for this species. Our study of the nests of *T. parvus* reveals a relatively small amount of cleptoparasitism by the miltogrammine fly, *Senotainia trilineata*. Perhaps the low, rapid provisioning flight and the rather deep nest of *T. obductus* serve as deterrents to fly cleptoparasitism. The “wagging” provisioning flight, rapid “escape” flight, “freeze-stop” (Alcock, 1975), “butt” (Lin, 1963), “knock-down” and sting, coupled with the relatively deep, tortuous nest of *T. parvus* undoubtedly serve to reduce the amount of cleptoparasitism by miltogrammine flies on this species.

The nests of both species of *Tachytes* are somewhat variable in configuration and size. Unfinished nests of *T. obductus* may contain up to six cells (Kurczewski and Kurczewski, 1971), whereas those of *T. parvus* may be 8-celled. Multicellular nests are the rule in species of *Tachytes* (Evans and Kurczewski, 1966). Nests of members of the *abdominalis* group tend to be more lateral and less vertical in composition than those of species belonging to the *aurulentus* group (Evans and Kurczewski, 1966; Kurczewski and Ginsburg, 1971). The main burrows of *T. obductus* and *T. parvus* may be as long as 47 and 59 cm, respectively. Cell depth in both species varies, seemingly with soil type (friability) and amounts of moisture and vegetation. For example, in *T. parvus* the shallowest nests (cells) were constructed in moderately to highly vegetated, moist, gravelly soil while the deepest nests (cells) were situated in bare, dry, loose sand. In *T. parvus* the cells furthest from the entrance in a nest are provisioned first and those nearest the entrance, last. In nests of both *T. obductus* and *T. parvus* a short spur often bifurcates from just below the entrance. Whether or not this space serves as a sleeping “chamber” for the wasp, a distractor for cleptoparasites, such as *Phrosinella aurifacies*, or simply represents a portion of the preexisting depression from which the nest is begun is unknown.

The cells in the nests of both species are similar in shape and size, with those of *T. obductus* being slightly larger. In the present study females of *T. obductus* were slightly larger and heavier ($\bar{x}$ = 45 mg) than those of *T. parvus* ($\bar{x}$ = 35 mg) and this size differential may account for differences in the provisions of the cells. Thus *T. obductus* selects a mix of adult and nymphal tetrigids (*Tetrix ornata*, *Paratettix cucullatus*) (Kurczewski and Kurczewski, 1971; Kurczewski, 1976), whereas *T. parvus* stores almost 100% nymphal *Tetrix ornata*. Kurczewski and Kurczewski (1971) reported nymphal *Neotettix femoratus* (Scudder) as prey of *T. parvus* (= *T. pattoni*) in coastal North Carolina. Reflecting this differential use of adults/nymphs, *T. obductus* stored 3–7 ($\bar{x}$ = 4.3) prey per cell, averaging 26.2 mg each (includes prey transport specimens and incompletely and fully-provisioned cells from this study and that of Kurczewski, 1976), for a total prey weight per cell of 104.8 mg (includes fully-provisioned cells from this study and that of Kurczewski, 1976), whereas *T. parvus* provisioned with 4–9 ($\bar{x}$ = 6.0) prey per cell, averaging 13.8 mg each (includes prey transport specimens and fully-provisioned cells from this study), for a total prey weight per cell of 88.4 mg (includes only fully-provisioned cells from this study).

The placement of prey in the cells of both species is identical, i.e. mostly head inward and ventral side upward but also in various other positions. In both species the egg is laid on a "medium-sized" grouse-locust in the cell. The egg-bearing tetrigid is often positioned atop other prey near the top of the cell. The shape, size and placement of the egg is essentially identical in the two species and the placement seems to be consistent with that of other species of *Tachytes* that have been studied (Krombein and Kurczewski, 1963; Evans and Kurczewski, 1966; Kurczewski and Ginsburg, 1971; Kurczewski and Kurczewski, 1984).

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**RESPONSE OF GERMAN COCKROACHES TO A DISPERSANT AND
OTHER SUBSTANCES SECRETED BY CROWDED
ADULTS AND NYMPHS (BLATTODEA: BLATTELLIDAE)**

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Abstract.—The responses of adult male German cockroaches to filter papers conditioned by crowded adult males and by large nymphs is compared to their response to female-conditioned papers. Males were repelled only from the latter papers. The lack of repellency to papers conditioned by males and large nymphs may be attributed to insufficient amounts of a dispersant pheromone to counteract the response to aggregation pheromone.

Chemical cues mediate defensive, reproductive, and social behaviors in insects. For example, aggregations are pheromonally induced in the crickets *Ceuthophilus secretus* (Nagel and Cade, 1983), *Acheta domestica* (Sexton and Hess, 1968; McFarlane et al., 1983), locusts (Gillett, 1968) and the cockroach, *Blattella germanica* (L.) (Bell et al., 1972; Ishii, 1970; Ishii and Kuwahara, 1967; Rust and Appel, 1985). In *A. domestica* (Sexton et al., 1968) and *B. germanica* (Suto and Kumada, 1981), the response to aggregation pheromone is countered by repellent effects of a dispersant which, in *A. domestica*, is secreted by both adult males and females. In *B. germanica* the dispersant was detected in bioassays where filter paper was conditioned by crowding adults of both sexes. Further study indicated the dispersant is present in oral secretions and is probably a proteinaceous substance(s) (Nakayama et al., 1984).

Nymphs of all stages, adult males, and gravid and non-gravid females were repelled from papers conditioned by crowded adult females, indicating all members of a population would respond to the dispersant (Ross and Tignor, 1985). The purpose of the present experiment was to determine whether cockroaches would also be repelled from papers conditioned by crowded adult males or large nymphs and to compare the response to that from female-conditioned papers. Adult males were used to test for repellency because they showed a particularly strong response to female-conditioned papers (Ross and Tignor, 1985).

MATERIALS AND METHODS

Cockroaches were drawn from the VPI wild-type strain. It has been maintained in our laboratory for approximately 160 generations. The laboratory is on a 14D/10L photocycle with temperature range of 24–27°C. Our bioassay technique was patterned after that of Ishii et al. (1967) and Suto and Kumada (1981). It differed from the experimental design we used to test response of different age/sex classes

to female-conditioned paper (Ross and Tignor, 1985) in that data were recorded by visual observation rather than photography and bioassays were conducted in the laboratory rather than a dark chamber. Therefore, to make results from crowded adult males and large nymphs as comparable as possible to those from females, an additional experiment was conducted with crowded adult females.

Three filter papers were used in the bioassays. One was conditioned by 40 adult males, one by 50 large nymphs (6th instar), and the third was unconditioned (control). Conditioning was done during the first 2–3 h of the light period by holding either the adult males or large nymphs for 1 h in a plastic vial (2.9 diam. $\times$ 5.5 cm in height) that contained a strip of Whatman no. 1 filter paper (3.8 $\times$ 7.0 cm) folded into a W-shape. The conditioned and control papers were placed on end equal distances between edges on the bottom of a glass battery jar (14.5 diam. $\times$ 19.5 cm in height). Papers were attached to the jar using a small drop of Liquid Paper®. Their positions were randomized. The jar top was covered with cheese cloth and the exterior of the jar with paper towels. Tests were begun immediately after conditioning. Twelve 2–3 week-old adult males were released into the jar. Their distribution was recorded visually at 30 min intervals during a period of 4 h. The experiment was replicated 18 times. Comparable data on response to papers conditioned by adult females were obtained by conditioning one paper with 30 gravid and the other with 30 7–10 day-old non-gravid females (probably mated). Otherwise the procedures were the same as above. Conditioning by larger numbers of males and nymphs than females assured a near equal degree of spatial crowding since their body size is somewhat smaller than that of females.

The data were subjected to arcsine and analyzed using Tukey's studentized range test (Sokal and Rohlf, 1969). Analysis was on the mean percent of males on the three papers through the period from 90 to 240 min because it took approximately 90 min for the adult males to settle on the filter papers.

RESULTS AND DISCUSSION

Figs. 1 and 2 show that most of the males were on filter papers, as expected since German cockroaches prefer vertical to flat surfaces (Bell et al., 1972; Rust and Appel, 1985). They were neither strongly attracted to nor strongly repelled from papers conditioned by large nymphs and other adult males (Fig. 1). In contrast, the majority of the males were on the control paper in the experiment with papers conditioned by gravid and non-gravid females (Fig. 2), indicating they were repelled from the conditioned papers (mean 94.9% on the control period through the period from 90–240 min; $P < 0.05$). Although Fig. 1 shows a more equal distribution of males, the mean proportion on paper conditioned by large nymphs ($36.4 \pm 2.8\%$ SE) was significantly higher than that on either the male-conditioned ($23.3 \pm 2.2\%$ SE) or control ($20.8 \pm 2.8\%$ SE) papers (90 $<$ time $<$ 240 min). The proportions on the male-conditioned and control papers did not differ significantly. The similarity between these estimates reflects a tendency for a larger cluster of males to occur on the control paper with equal frequency to the conditioned paper, rather than a 50:50 division between the distribution of individuals with each replicate. For example, in 13 of 18 replicates, $>75\%$ of the males in these locations were on one or the other paper.

The lack of repellency of paper conditioned by large nymphs and adult males seems contradictory to experiments of Nakayama et al. (1984) that indicated adult

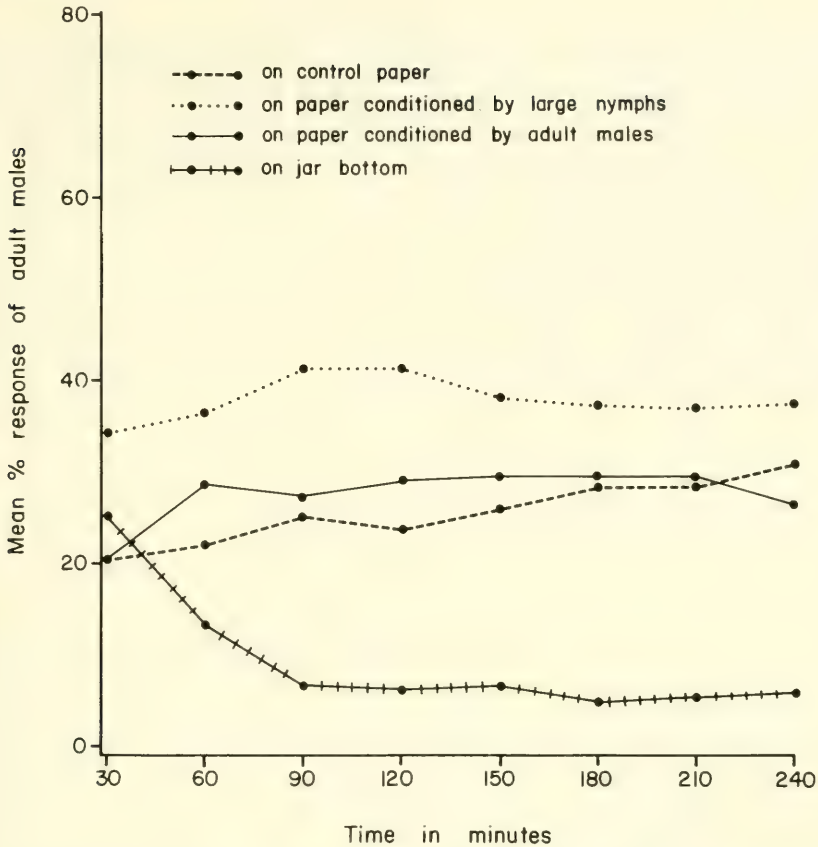


Fig. 1. Distribution of adult male *B. germanica* in battery jars containing filter papers conditioned by crowding adult males and large nymphs and an unconditioned (control) paper.

males and large nymphs secrete the dispersant. However, their procedures differed from those used here in the following respects: the response of small nymphs, rather than adult males, was tested; larger numbers were used to obtain the dispersant; and the papers were not conditioned directly by the insects. The former two differences probably did not contribute to the apparent discrepancy. German cockroaches respond to the dispersant regardless of age/sex class (Ross and Tignor, 1985). The effects of increased crowding have not been completely explored, but no indication of repellency was found in preliminary tests with extreme crowding of adult males (Ross and Tignor, unpubl.). For example, of 90 small nymphs tested against a control and a paper conditioned by 75 males, 59% were on the conditioned paper. On the other hand, the differing results can be explained readily by conditioning procedures. Nakayama et al. (1984) rinsed jars contaminated by crowded insects with Tris-HCl buffer, followed by extraction in ethyl ether. The remaining "aqueous solution" was used to condition papers. Aggregation pheromone is removed in ethyl ether (Ishii and Kuwahara, 1967). We infer that the results of our experiments reflect response to a combination of dispersant and aggregation pheromone, whereas those of Nakayama et al. (1984) tested for dispersant emission.

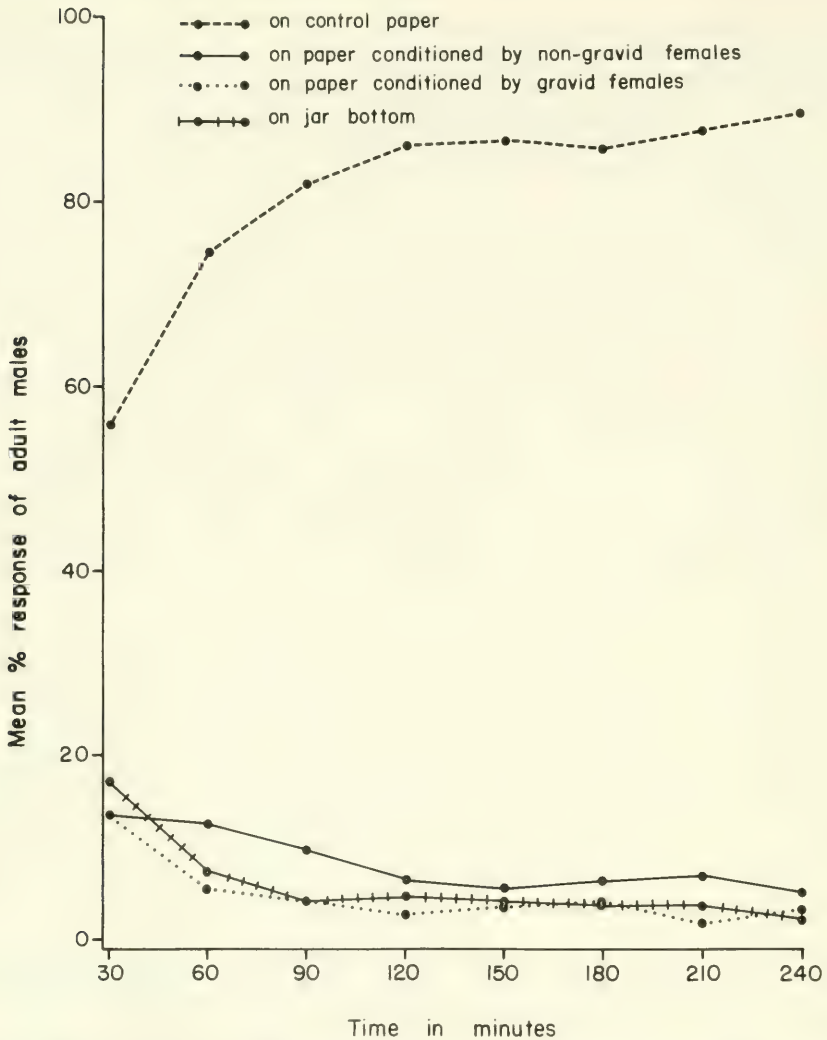


Fig. 2. Distribution of adult male *B. germanica* in battery jars containing filter papers conditioned by crowding gravid and non-gravid females and an unconditioned (control) paper.

The results reported here leave little doubt that the repellency of papers conditioned by adults in Suto and Kumada's (1981) bioassays was due solely to the secretion of the dispersant pheromone by adult females. Conditioned filter papers showed the characteristic wetness that Suto and Kumada associated with secretion of the dispersant. However, this secretion was repellent only in the case of female-conditioned papers. Unfortunately, Suto and Kumada's evidence that adults secrete aggregation pheromone "irrespective of population density" does not shed light on the relative roles of aggregation pheromone and the dispersant in the observed differences between the response to female- and male-conditioned papers. The possibility that adult females secreted such large amounts of the dispersant that response to aggregation pheromone was over-ridden cannot be distinguished from the alternate possibility that they ceased or decreased secretion

of aggregation pheromone when crowded. Likewise, the absence of a detectable response of adult males to male-conditioned paper could have several explanations. They secrete aggregation pheromone under presumably uncrowded conditions (Ishii and Kuwahara, 1967) and are capable of producing the dispersant (Nakayama et al., 1984). Possibly neither substance was present on conditioned paper in an amount sufficient to obscure response to the other substance. Alternatively, it may be that adult males cease secretion of both pheromones when crowded. The attraction of males to paper conditioned by large nymphs was almost certainly a response to aggregation pheromone. The confinement of the insects in a small vial ensured a fairly intense level of crowding, yet only the adult females secreted sufficient dispersant to elicit a repellent effect. We suggest that adult females give the signal that causes aggregations to disperse from crowded and perhaps other stressful conditions.

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NEW SPECIES OF CADDISFLIES (TRICHOPTERA)
FROM ALABAMA

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Abstract.—Five new species of Trichoptera, *Agapetus alabamensis* (Glossosomatidae), *Ochrotrichia elongiralla* (Hydroptilidae), *Theliopsyche tallapoosa* and *Lepidostoma weaveri* (Lepidostomatidae), and *Nectopsyche paludicola* (Leptoceridae) are described and illustrated.

In the course of a continuing survey of the caddisflies of Alabama, five undescribed species were collected. These new species, one each in the genera *Agapetus*, *Ochrotrichia*, *Theliopsyche*, *Lepidostoma*, and *Nectopsyche* are described and diagnosed herein.

Agapetus are represented in all faunal regions, except the Neotropical, with 30 species known from North America (Wiggins, 1977, 1984). *Ochrotrichia* and *Nectopsyche* are both restricted to the New World, with 45 and 12 species, respectively, reported from North America (Haddock, 1977; Blickle, 1979). North American species of the Holarctic genus *Lepidostoma* number 75, while *Theliopsyche*, which occur along the Appalachian Mountains are represented by 5 species (Weaver, 1983).

Adults of the new species of *Ochrotrichia*, *Theliopsyche*, and *Nectopsyche* were collected with a UV light trap, while adults of *Agapetus* and *Lepidostoma* were primarily obtained by sweeping or by rearing of pupae taken from streams. Terminology generally follows that of Schmid (1980). Type material will be deposited at the National Museum of Natural History (USNM), Illinois Natural History Survey (INHS), Royal Ontario Museum (ROM), University of Alabama (UA), Florida State Collection of Arthropods (FSCA), and the personal collection of the author.

Agapetus alabamensis Harris, NEW SPECIES

Fig. 1

In many aspects, this species resembles *A. illini* Ross. It differs primarily in the pronounced serrations at the apex of segment X, the rectangular shape of the inferior appendages, and the lack of dorso-lateral spines at the base of segment X.

Male.—Length 4.5–4.6 mm. Body and wings dark brown, legs yellow. Antennal segments 26. Abdominal segment VI with ventro-mesal process extending to posterior segment VIII. Segment IX generally ringlike in lateral view, fused with segment X dorsally. Preanal appendages nearly half length segment X, in lateral

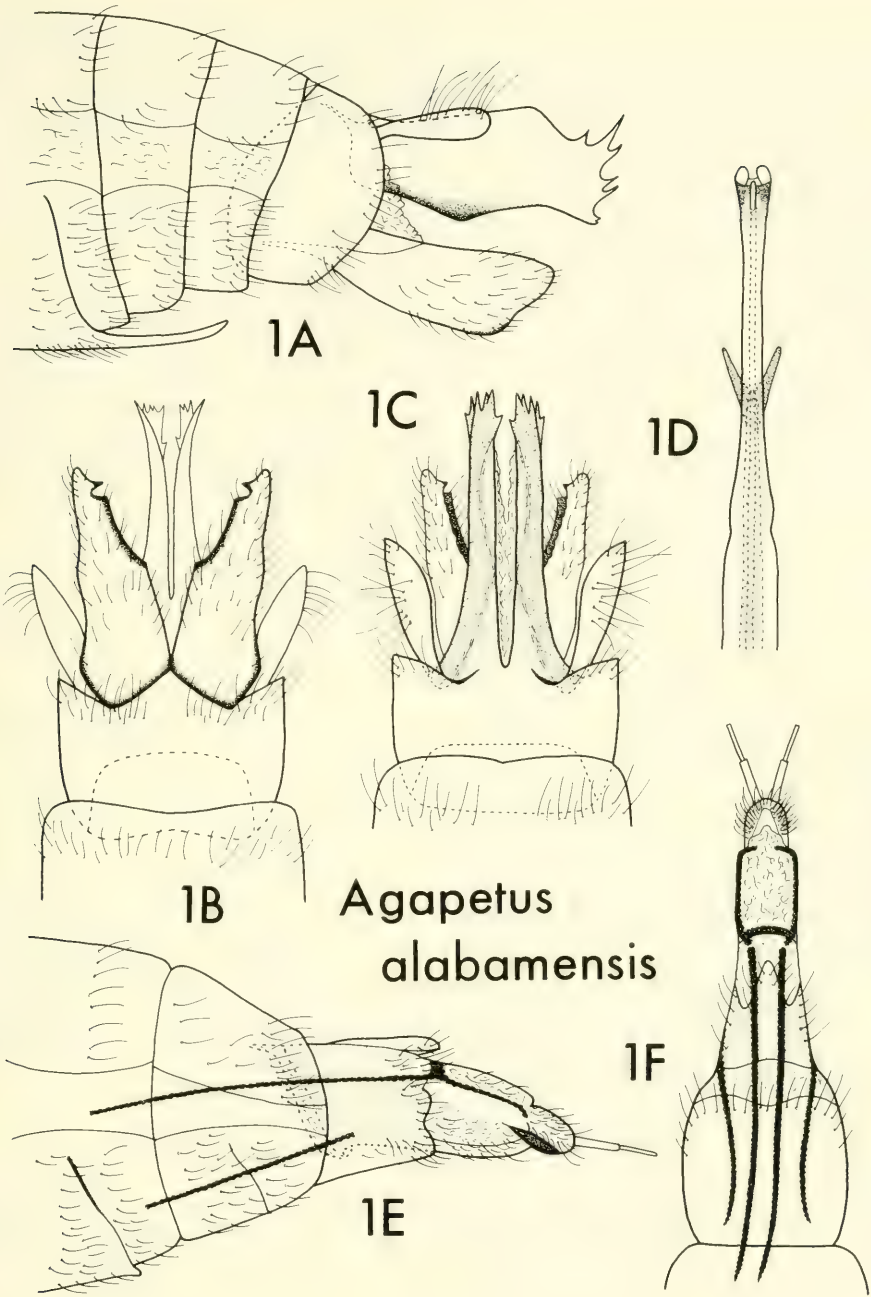


Fig. 1. *Agapetus alabamensis* n. sp., male and female genitalia. 1A, Lateral view ♂. 1B, ventral view ♂. 1C, Dorsal view ♂. 1D, Phallus. 1E, Lateral view ♀. 1F, Dorsal view ♀.

view claviform and originating near dorsum, in dorsal view generally oblong, with basomesal margin convex, and slightly diverging laterally. Segment X membranous dorsally, sclerotized ventrally; in dorsal view narrow and parallel-sided, divided into two arms distally with heavy serration at each apex; in lateral view these serrations appearing as five large spines projecting dorsally and a small pair of ventral spines projecting posteriorly. Inferior appendages nearly rectangular in lateral view, widened and obliquely truncate posteriorly; in ventral view each triangular with sclerotized spine subapically at ventro-mesal margin. Phallus typical for genus, elongate, tapering distally, with apex bilobed.

Female.—Length 4.6–4.8 mm. Overall appearance similar to male. Abdominal segment VI with short ventro-mesal process. Segment VII ringlike. Segment VIII with dorsal lobe protruding posteriorly, pleural margin incised; two pair of apodemes, dorsal pair originating near posterior margin and ventral pair originating at anterior margin. Segment IX lost. Segment X rectangular in dorsal view, membranous, with pair of apodemes along dorso-lateral margin connected anteriorly by heavily sclerotized dorsal bridge. Segment XI ovoid, dorsum membranous, venter sclerotized, with pair of two-segmented cerci.

Immatures.—Both larvae and pupae have been associated for the species, via rearing and the collection of pharate adults. Since immatures of most *Agapetus* species are unknown, a description is not provided herein. The immatures will be deposited for future studies at USNM, INHS, ROM, and UA.

Eymology.—Latin: of Alabama.

Holotype ♂.—Alabama, Tuscaloosa County, unnamed tributary to Wallace Branch, 5 mile southeast Berry (R10W, T17S, S2), 26 April 1984, S. Harris (USNM).

Paratypes.—Alabama, same as above, 9 ♂, 16 ♀ (USNM, INHS, ROM); same, but 11 April 1984, 1 ♂ (UA); same, but 16 May 1984, 2 ♂ (FSCA).

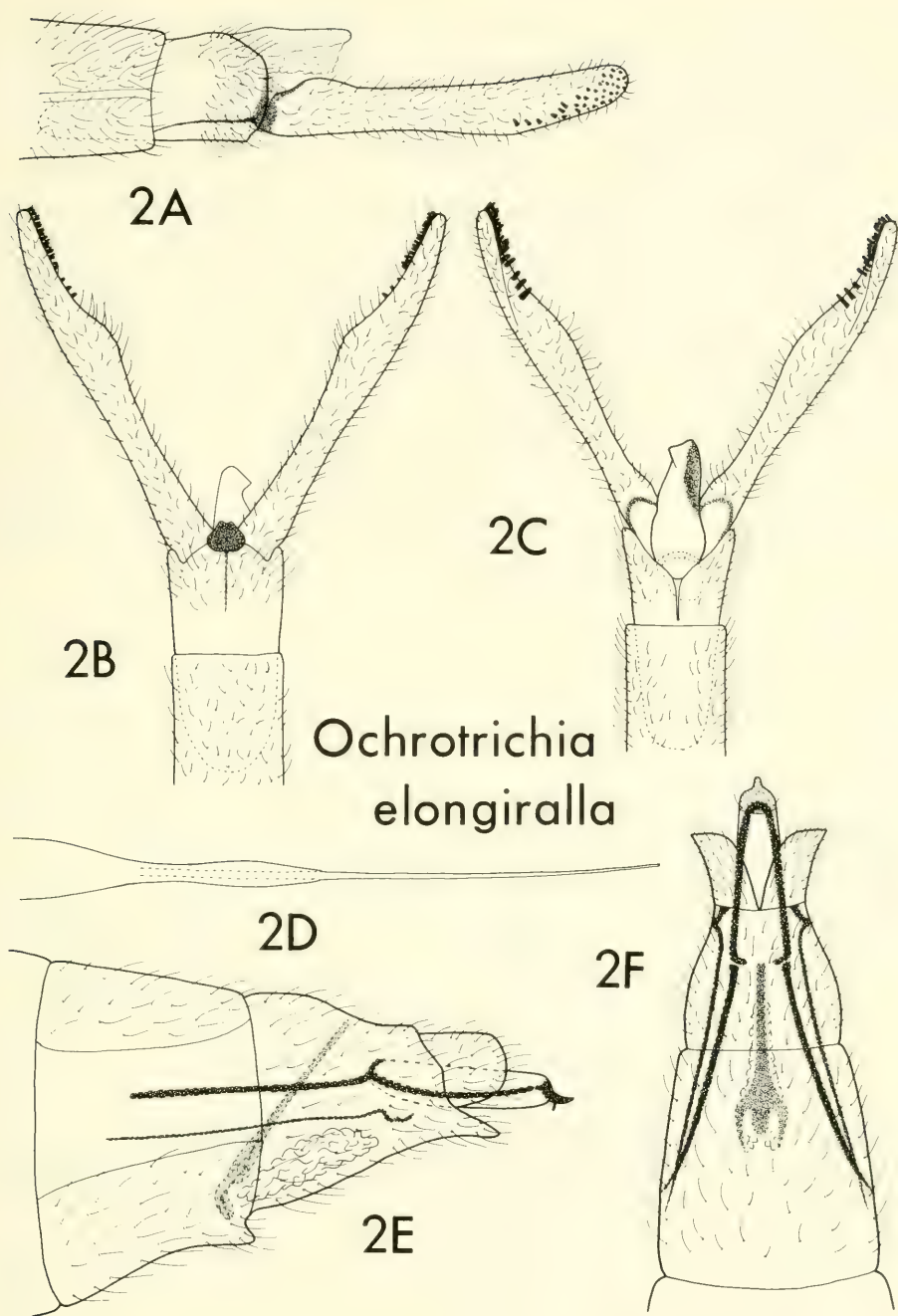
Remarks.—*Agapetus alabamensis* is most easily distinguished from *A. illini*, which it resembles, on the basis of the terminal spines of segment X. In *A. illini*, these spines are minute and numerous, while in *A. alabamensis* the spines are few and elongate. *Agapetus alabamensis* has only been collected in a small, temporary stream of the lower Cumberland Plateau. Final instar larvae were collected in March, with pharate adults present in April. Two specimens were collected in UV light traps operated along the stream in May.

Ochrotrichia elongiralla Harris, NEW SPECIES

Fig. 2

In general appearance, this species resembles *O. xena* Ross. It differs primarily in the elongate, narrow inferior appendages and in the rounded posterior of segment X.

Male.—Length 4.1–4.8 mm. Antennal segments 26. Forewings brown, with narrow, transverse white band at midlength. Abdominal segment IX generally trapezoidal, narrowing anteriorly in lateral view; deeply incised dorsally; ventrally with heavy, cordate postero-mesal sclerite, narrowly incised laterally. Segment X short, truncate in lateral view, lightly sclerotized dorsally, membranous ventrally; in dorsal view, round basally narrowing to rounded apex with beaklike protrusion subapically on mesal margin, lightly sclerotized subapically along lateral margin.



Ochrotrichia
elongiralla

Fig. 2. *Ochrotrichia elongiralla* n. sp., male and female genitalia. 2A, Lateral view ♂. 2B, Ventral view ♂. 2C, Dorsal view ♂. 2D, Phallus. 2E, Lateral view ♀. 2F, Dorsal view ♀.

Inferior appendages long and slender, in lateral view nearly 4 times as long as segment X, base of appendages about same thickness as segment X, subapically with numerous short, black pegs on mesal surface; in dorsal and ventral view, appendages diverging with ridge at $\frac{3}{4}$ length, each narrowing to rounded apex bearing thick pegs at dorso-mesal margin. Phallus long and thin, widening and tapering basally.

Female.—Length 3.5–5.5 mm. Antennal segments 25. Overall appearance similar to male. Abdominal segment VI quadrate with short ventro-mesal process. Segment VII rounded laterally in dorsal view; in lateral view trapezoidal in shape, with postero-ventral lip; internally with two pair of apodemes, narrow lateral pair originating at posterior margin and extending anteriorly to beyond middle of segment VI, thicker mesal pair originating near middle segment VII, diverging and extending anteriorly to beyond middle of segment VI. Segment VIII deeply cleft dorsally and diverging; in lateral view reduced and rounded distally. Segment IX narrow and retracted into segment VII with pair of lateral apodemes. Segment X short, with small nipple at apex bearing two short setae at antero-lateral margin; in lateral view with heavy acute sclerite at apex. Vaginal apparatus fork-shaped; elongate and parallel-sided postero-dorsally, divided into two acute lateral prongs and round mesal lobe antero-ventrally.

Immatures.—Unknown.

Etymology.—Latin: “elongate and slender” referring to the general appearance of the species.

Holotype ♂.—Alabama, Madison County, Big Cove Creek at Dug Hill Road, 5 miles east Huntsville, 3 June 1984, S. Harris (USNM).

Paratypes.—Alabama, same as above, 78 ♂, 25 ♀ (USNM, INHS, UA, FSCA).

Remarks.—*Ochrotrichia elongiralla* is separated from *O. xena*, which it closely resembles, on the basis of the inferior appendages and shape of segment X. In *O. xena*, the inferior appendages are approximately 2 times the length of segment X and wide at base; in *O. elongiralla* the inferior appendages are nearly 4 times the length of segment X and narrow at base. Segment X is acute apically in *O. xena* and rounded apically in *O. elongiralla*. *Ochrotrichia elongiralla* has only been collected along a small, gravel-bottom stream in the Highland Rim Plateau.

Theliopsyche tallapoosa Harris, NEW SPECIES

Fig. 3

This species is most similar to *T. grisea* (Hagen) on the basis of the well developed dorsal process of the inferior appendage. However, while this process is long and linear in *T. grisea*, in *T. tallapoosa* the process is short, curved, and acuminate.

Male.—Length 5.2 mm. Brown in color, with dorsum of head and thorax slightly darker. Head typical for genus, antennal scape 0.4 mm long, maxillary palp 0.5 mm in length. Wings typical for genus, brown with several irregularly shaped white spots; forewings with dense, short black hairs basally; hind wings with long brown hairs basally, along anal vein and at the posterior margin. Legs and abdomen brown. Segment VII with paddle-shaped ventro-mesal process. Segment IX roughly trapezoidal in lateral view; broadly excised dorsally. Segment X about $\frac{1}{2}$ length of inferior appendages, in dorsal view deeply incised, bearing pair of long setae at apex, four pair mesal setae basally; intermediate appendages spini-

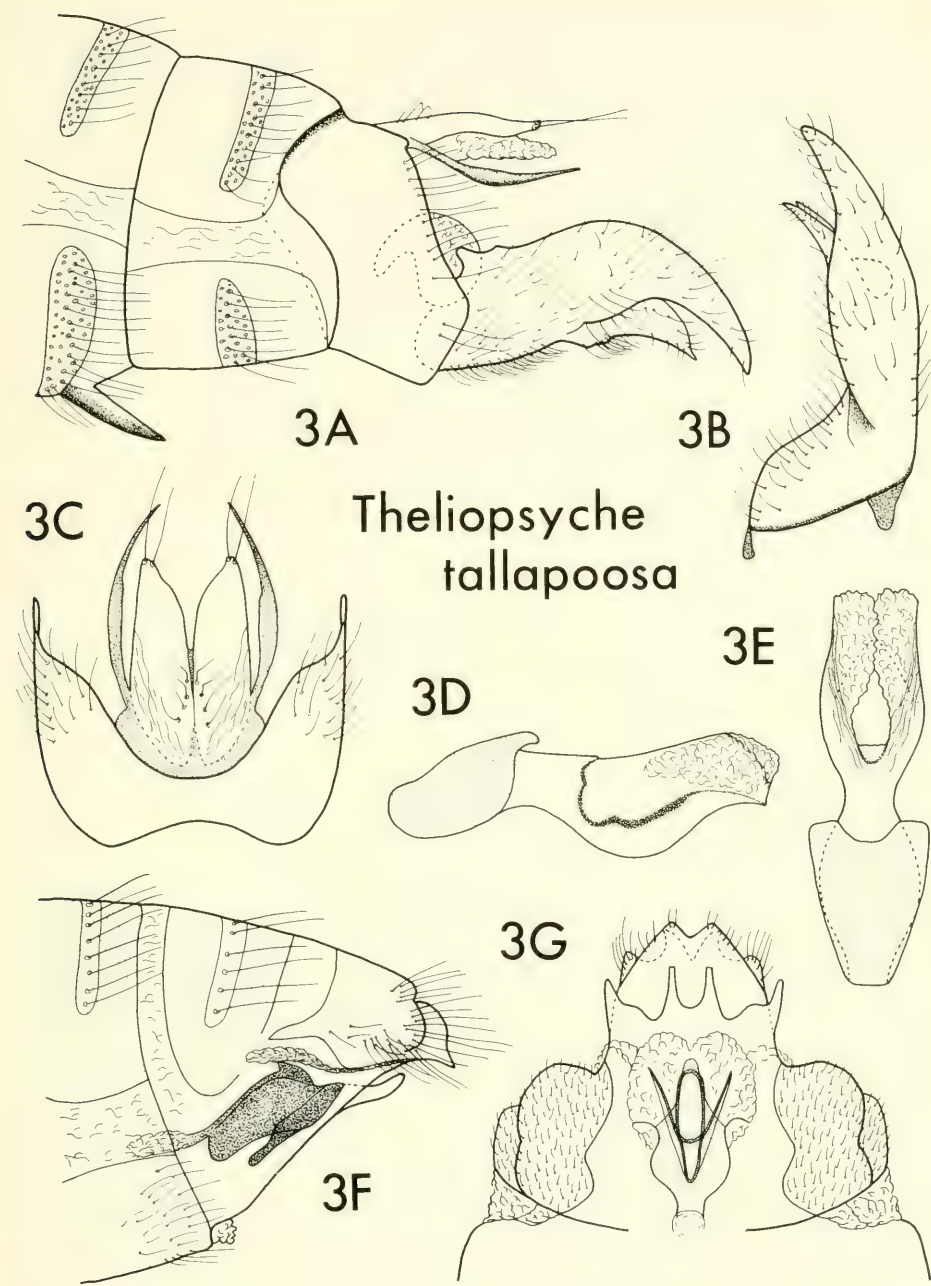


Fig. 3. *Theliopsyche tallapoosa* n. sp., male and female genitalia. 3A, Lateral view ♂. 3B, Inferior appendage ♂, dorsal view. 3C, Dorsal view ♂. 3D, Phallus, lateral view. 3E, Phallus, dorsal view. 3F, Lateral view ♀. 3G, Ventral view ♀.

form and sclerotized. Inferior appendages each with dorsal process thickened and elongated slightly beyond ventral process, in lateral view dorsal process curving ventrad to acute apex. Phallus sinuate with narrow phallotremal sclerite, parameres absent, phallobase obscured by sclerotized phallic shield.

Female.—Length 5.2 mm. Overall appearance similar to male. Antennal scape 0.5 mm in length, maxillary palp 0.8 mm long. No sexual dimorphism evident in wings. Posterior margin of sternite VII with four raised points in ventral view. Vaginal apparatus with anteriorly directed spermathecal sclerite in ventral view, pair of membranous lobes extending posteriorly, short rounded process at center. In lateral view spermathecal process generally oblong, narrowing posteriorly.

Immatures.—Unknown.

Etymology.—Named for Tallapoosa County.

Holotype ♂.—Alabama, Tallapoosa County, Timbergut Creek, downstream crossing Hwy. 22, 19 May 1984, S. Harris and P. Lago (USNM).

Paratypes.—Alabama, same as above, 1 ♂, 1 ♀ (USNM).

Remarks.—*Theliopsyche tallapoosa*, along with *T. grisea*, is separated from other *Theliopsyche* by the expanded dorsal process of each inferior appendage. However, while this process is elongate and narrow in *T. grisea*, in *T. tallapoosa* the process is short and acuminate. Larvae of *Theliopsyche* are thought to inhabit springs and springruns (Wiggins, 1977; Weaver, 1983), however, *T. tallapoosa* was collected along a small (6 m wide), swift Piedmont stream, with rocky bottom.

Lepidostoma weaveri Harris, NEW SPECIES

Fig. 4

This species is similar in general appearance to *L. swannanoa* Ross and *L. compressum* Etnier and Way. However, the structure of segment X and the inferior appendages render the species distinct.

Male.—Length 6.8–7.8 mm. Body, wings, and appendages light brown, head and thorax slightly darker brown. Antennal segments 40, with scape 0.6 mm long. Maxillary palp 1.3 mm in length. Wings with no obvious sexual dimorphism. Abdominal segment IX quadrate laterally, dorsally broadly incised at anterior margin. Segment X in dorsal view fused with segment IX anteriorly, posteriorly divided into two converging lateral arms, each rounded apically and tipped with several stout setae; in lateral view domed baso-dorsally, narrowed and abruptly upturned distally. Inferior appendages each divided into a thin dorsal and thick ventral process, appearing nearly equal length in lateral view, ventral process with short, thin mesal harpago subapically; in ventral view dorsal process strongly curved, narrow basally, widening slightly apically, ventral process wide basally, narrowing to rounded apex and extending slightly beyond dorsal process. Phallus with phallobase extending dorsally over phallicata in pair of membranous lobes, phallicata bulbous, phallotremal sclerite round laterally, curved dorsally, parameres absent.

Female.—Length 7.2–8.2 mm. Overall appearance similar to male. Antennal segments 40, with scape 0.6 mm long. Maxillary palp 1.1 mm in length. Abdominal segment VIII with tergite quadrate, sternite reduced with posterior margin emarginate. Segment IX with small dorso-lateral sclerite. Segment X reduced to pair of small lobes posteriorly, fused anteriorly with segment IX. Vaginal apparatus diamond-shaped ventrally, with narrow keyhole-shaped postero-ventral process.

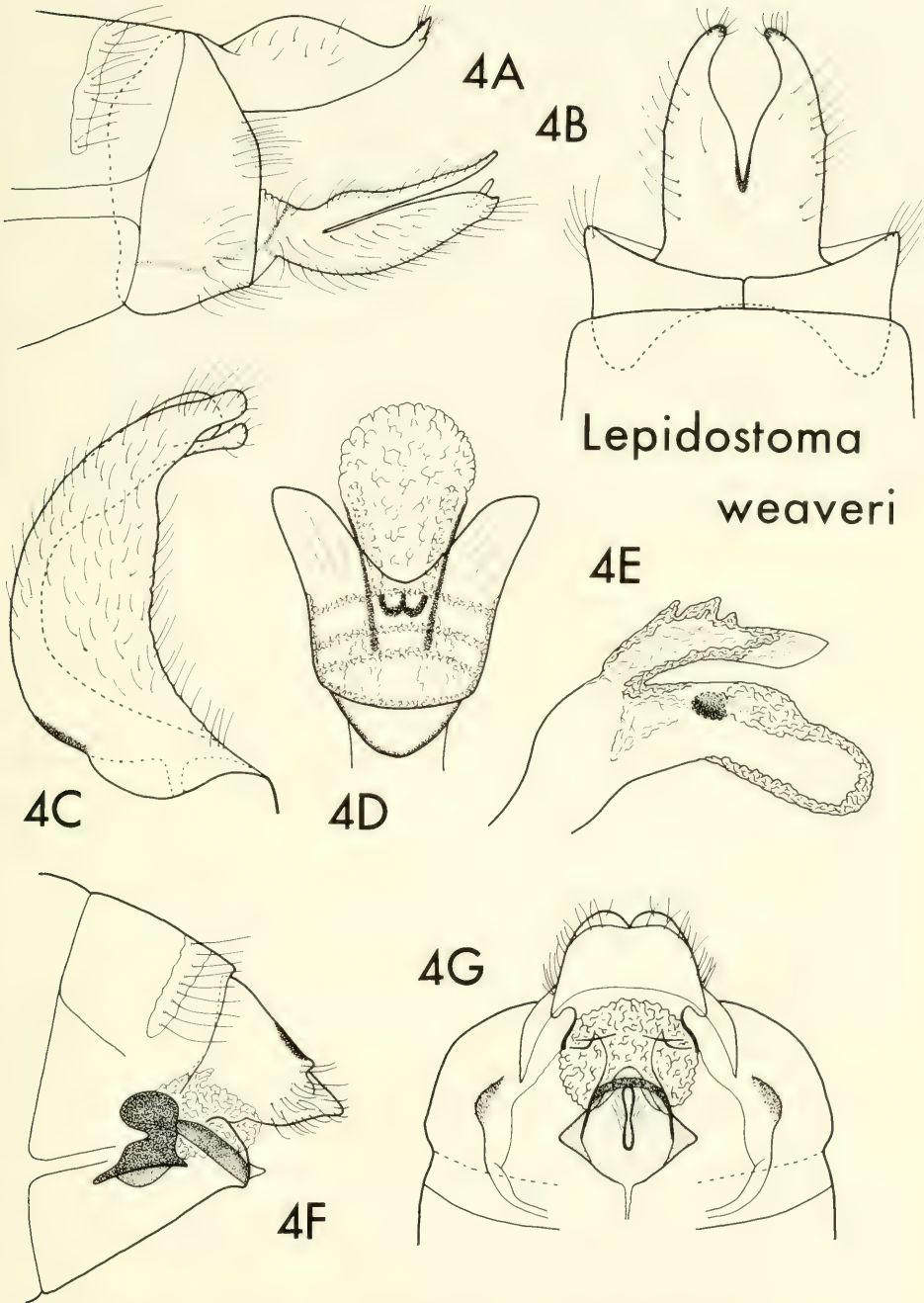


Fig. 4. *Lepidostoma weaveri* n. sp., male and female genitalia. 4A, Lateral view ♂. 4B, Dorsal view ♂. 4C, Inferior appendage ♂, ventral view. 4D, Phallus, dorsal view. 4E, Phallus, lateral view. 4F, Lateral view ♀. 4G, Ventral view ♀.

In lateral view generally trapezoidal in shape, incised anteriorly, posteriorly with thin ventral band.

Immatures.—Both larvae and pupae have been associated for the species, via rearing of adults. Using the key presented by Weaver (1983), larva fall in the subgenus *Nosopus*, on the basis of the panel-type leaf case with parallel sides and length of the postmentum being greater than the ecdysal line. Final instar larvae were collected in February and March. Since so few of the *Lepidostoma* species have associated immatures, descriptions of the larvae and pupae are not included herein. The immatures will be deposited for future reference at USNM, INHS, ROM, and UA.

Etymology.—Named for John S. Weaver, III in recognition of his studies on the Lepidostomatidae.

Holotype ♂.—Alabama, Tuscaloosa County, unnamed tributary to Tyro Creek at bridge 303, 4.5 mile east New Lexington (R10W, T17S, S15), 12 March 1984, S. Harris (USNM).

Paratypes.—Alabama, same as above, 7 ♂, 2 ♀ (USNM, INHS, UA), same, but 14 March 1984, 2 ♂, 4 ♀ (USNM, INHS, FSCA), same, but 15 March 1984, 3 ♂, 10 ♀ (USNM, INHS, UA, ROM), same, but 13 March 1984, 3 ♂, 2 ♀, same, but 19 March 1982, 1 ♂, unnamed tributary to Wallace Branch, 5 mile southeast Berry (R10W, T17S, S2), 15 March 1984, S. Harris, 3 ♂, 1 ♀ (USNM, INHS).

Remarks.—Many of the characters of the male genitalia of *L. weaveri* appear to be intermediate between those of *L. compressum* and *L. swannanoa*. Segment X resembles that of *L. compressum* in its sinuate lateral appearance, although in *L. compressum* the distal arms are much longer and the dorsal incision much deeper. In *L. swannanoa*, segment X is wedge-shaped laterally and serrate at the dorso-lateral margins. This serration is lacking in *L. weaveri* and *L. compressum*. The inferior appendages of *L. weaveri* are similar to those of *L. swannanoa*, although in *L. swannanoa* the dorsal process is expanded more apically than in *L. weaveri*. In *L. compressum* this dorsal process is more elongate than in either *L. weaveri* or *L. swannanoa*. The structure of the phallus and the female genitalia are similar in *L. weaveri* and *L. swannanoa*. As with *Agapetus alabamensis*, *L. weaveri* is restricted to several small, spring-flowing, temporary streams on the Cumberland Plateau. Adults were collected by sweeping along the stream in March and by rearing pupae.

Nectopsyche paludicola Harris, NEW SPECIES

Figs. 5–6

The narrow base of the inferior appendage aligns this species with *N. exquisita* (Walker) and *N. candida* (Hagen). However, the overall appearance of the inferior appendage is more stout than in either *N. exquisita* or *N. candida*. In addition, *N. paludicola* differs in having brown wings.

Male.—Length 7.5–9.0 mm. Head and thorax, dark brown with profuse white hair dorsally and dorso-laterally. Eyes small, about $\frac{1}{3}$ interocular width in dorsal aspect. Antennae long (approximately 76 segments), with white bands fading distally. Legs light brown. Forewings gray to tawny, with indistinct brown spots along the veins and in cluster at apex, no coloration pattern evident with wings folded, long white hairs basally, short dark and white hairs spread over wing surface. Hind wings uniformly gray with conspicuous veins, surface covered with



Fig. 5. *Nectopsyche paludicola* n. sp., right forewing ♂.

short, dark hairs. Abdomen light brown with greenish hue, genitalia typical for the genus. Segment IX trapezoidal with short dorso-mesal process, preanal appendages (dorso-lateral arms) long, curving slightly ventrad and tapering to bulbous apex. Intermediate appendages of segment X extending to near apex of inferior appendages; in lateral view, these appendages wide basally, narrowing and parallel-sided distally. Inferior appendages oblique in lateral view, narrow at base, widening at apex with narrow sclerotized lateral thumb, ventral margin irregularly incised; ventro-mesal filaments thick and long with lateral accessory filament. Phallus typical for genus with large ventral plate and small phallotremal sclerite, external periphallic processes of phallic shield narrow with bulbous tip.

Female.—Length 7.0–7.5 mm. Overall appearance similar to male with genitalia typical for the genus. Segments IX and X fused, narrowly triangular in lateral view with appendages long and slender. Valves fingerlike. Vaginal vestibule long and cylindrical. Vaginal apparatus round in ventral view with pair of round, posterior plates; in dorsal view with narrow ventral keel.

Immatures.—While *Nectopsyche* larvae have been collected at the type locality, a positive association is not yet possible.

Etymology.—Latin: “marsh-dweller” referring to the habitat of the species.

Holotype ♂.—Alabama, Baldwin County, Farris Creek at Hwy. 59, 20 August 1984, S. Harris and M. Mettee (USNM).

Paratypes.—Alabama, same as above, 4 ♂ (USNM, INHS), same, but 3 July 1984, 2 ♂, 1 ♀, S. Harris (USNM), same, but 18 August 1983, 2 ♂, S. Harris and P. O’Neil, same, but 11 May 1982, 22 ♂, S. Harris (USNM, INHS, UA, FSCA), Red Hills Creek at Hwy. 59, 18 August 1983, 19 ♂, 22 ♀, S. Harris and P. O’Neil (USNM, INHS, UA, FSCA); Mobile County, Nobodies Creek, upstream crossing Co. Hwy. 96, 13 May 1982, 1 ♂, S. Harris, Little Creek, 2 miles southeast Citronelle, 12 May 1982, 2 ♂, S. Harris; Washington County, Okwakee Creek at Co. Hwy. 9, 13 May 1982, 8 ♂, S. Harris.

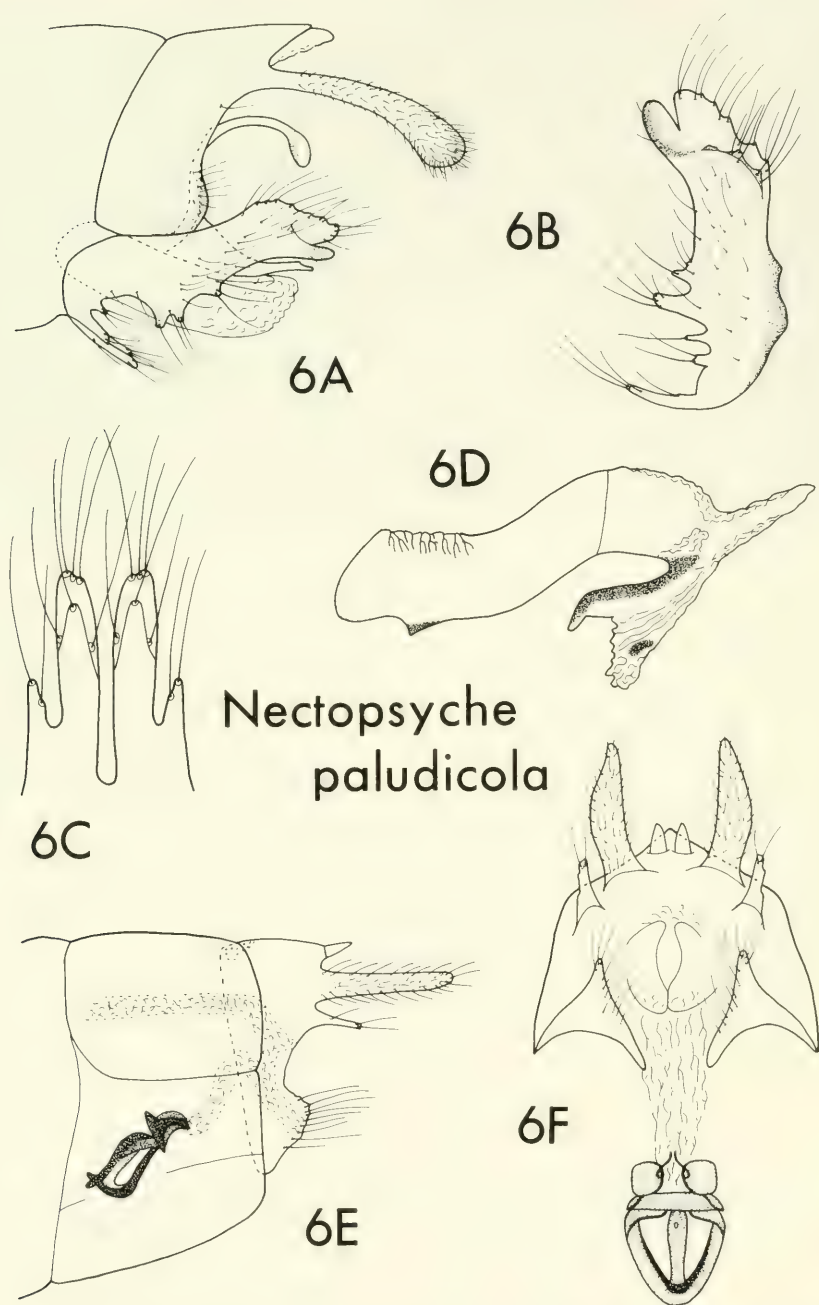


Fig. 6. *Nectopsyche paludicola* n. sp., male and female genitalia. 6A, Lateral view ♂. 6B, Inferior appendage ♂, lateral view. 6C, Genitalic filaments at base of inferior appendage, ventral view. 6D, Phallus, lateral view. 6E, Lateral view ♀. 6F, Ventral view ♀.

Remarks.—On the basis of the male genitalia, *N. paludicola* resembles *N. candida*, *N. exquisita*, and *N. tavana* (Ross). However, while all of these species have predominantly white wings, *N. paludicola* has brownish-gray wings. *Nectopsyche paludicola* has been collected primarily along small, sand-bottom streams draining *Juncus* marshes in coastal Alabama.

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The Geological Survey of Alabama provided facilities and supplies during the course of the study and are gratefully acknowledged. The following researchers graciously provided type material and specimens for comparisons. John Unzicker, *Lepidostoma compressum*, *Ochrotrichia xena*, *Agapetus illini*, and *Nectopsyche tavana*; Oliver Flint, Jr., *N. tavana*, *L. compressum*, and *L. swannanoa*; John Weaver, III, *Theliopsyche grisea*; David Etnier, *L. compressum*. John Morse and John Weaver, III kindly reviewed the manuscript. I thank also Paul Lago, Scott Mettee, Patrick O'Neil, and Earle Cross for their help in the collections; Sabra Rager for typing several drafts of the manuscript; Ruth Turner, Patrick O'Neil, and Harriett Smith-Somerville for their help with the photographs and figures; and Larry Davenport for identification of aquatic plants.

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ETHOLOGY OF *EFFERIA CRESSONI* WITH A REVIEW OF THE
COMPARATIVE ETHOLOGY OF THE GENUS
(DIPTERA: ASILIDAE)¹

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Abstract.—The behavior of *Efferia cressoni* (Hine) has been studied in Wyoming, U.S.A. and Mexico. This species exhibited similar behavior patterns in its widely separated habitats except for prey selection (type and size), presence or absence of male searching flights for receptive females with which to mate and daily rhythm of activity. All species of *Efferia*, for which detailed information is available, show similar behavior patterns with respect to foraging and feeding (foraging sites, prey capture methods, immobilization of prey, prey manipulation methods, and prey specificity), male courtship behavior (searching flights) and copulatory position (male over female). Differences in behavior among species of *Efferia* are primarily those of behavior during copulation, duration of copulation and oviposition site chosen. The latter is dependent on the shape of the female's ovipositor.

The genus *Efferia* is one of the largest among the Asilidae in the United States and Mexico comprising approximately 200 species (Martin, 1965; Martin and Papavero, 1970; Wilcox, 1966). However, behavioral data has been recorded for only 18 species. Some of this information is sketchy and provides limited data on prey specificity and/or foraging sites.

This paper summarizes the available data on this genus (Table 1) and presents information on the ethology of *E. cressoni* (Hine) near Guernsey, Wyoming, U.S.A. and Rancho Experimental "La Campana," Mexico (80 km north of Chihuahua). To our knowledge, this is the first time that behavioral observations have been made on a robber fly species in such widely separated habitats. The almost identical behavior for *E. cressoni* in the two habitats lends support to using behavioral observations as a taxonomic tool.

COMPARATIVE ETHOLOGY OF *EFFERIA CRESSONI*
IN WYOMING, U.S.A. AND MEXICO

Methods.—Methods for gathering and analyzing ethological data for *E. cressoni* in Wyoming were essentially the same as those described for *Neoitamus vittipes*

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(Macquart) in Lavigne (1982). Voucher specimens, on which *E. cressoni* behavioral observations are based, have been placed in the entomological collection of the National Museum of Natural History, Washington, D.C., as lot #52.

Behavioral observations on *E. cressoni* in Wyoming were carried out in Guernsey State Park between June 7 and 20, 1978. The robber fly population inhabited a rocky hillside (Fig. 1) and adjacent gully just west of Guernsey Reservoir. The study area vegetation is typical of that found on the high plains. Common plants included the grasses, *Bouteloua gracilis* (H.B.K.) Lag. ex Steud., *Sitanion hystrix* (Nutt.) J. G. Smith, *Stipa comata* Trin. Rupr., and the forbs, *Allium textile* Nels and Macbr., *Arenaria* sp., *Astragalus missouriensis* Nutt., *Artemisia frigida* Willd., *Gaura coccinea* Nutt. ex Pursh, *Lygodesmia juncea* (Pursh) D. Don, *Opuntia polyacantha* Haw., *Petalostemon candidus* (Willd.) Michx., *Sphaeralcea coccinea* (Pursh) Rhdb., *Tradescantia occidentalis* (Brit.) Smyth, and *Yucca glauca* Nutt.

Behavioral observations on *E. cressoni* in Mexico were reported in Lavigne and Dennis (1985). This species' habitat in Mexico was oak brush savannah in foothills below the Ponderosa Pine zone.

Distribution.—*Efferia cressoni* has not previously been reported as occurring north of Ft. Collins, Colorado. According to Wilcox (1966), this species occurs in Arizona, Colorado, New Mexico and Texas. Both Hine (1919) and Wilcox provided drawings of the superior (upper) forceps which is typically notched at the apex. Wilcox illustrates the lower forceps of the male genitalia with a dorsal, medial "thumb-like" projection or tooth. The male specimens from both Wyoming and Rancho Experimental "La Campana" have a more squared lower forceps and lack the medial projection. However, the ventral fringe of hairs resembles that illustrated by Wilcox.

Foraging and feeding behavior.—*Efferia cressoni* in both Wyoming and Mexico forage from soil, rocks and vegetation (Table 1), depending on the substrate surface temperature. At both locations this species foraged from the ground until the surface temperature reached 40 to 41°C and then they moved onto vegetation. In Mexico, *E. cressoni* forages from vegetation at heights ranging from 5 to 20 cm above the ground, whereas in Wyoming foraging occurred primarily at heights of 7.5 to 12.5 cm. Once *E. cressoni* moved to vegetation, they generally foraged from shaded areas. However, this behavior was not observed as frequently in Wyoming.

Efferia cressoni captured prey in flight at distances of 1 m or less. In Wyoming this species was observed to immobilize prey in flight. Immobilization of prey by *E. cressoni* in Mexico has not been observed.

During feeding *E. cressoni* hovered and manipulated prey with all six tarsi prior to reinserting its hypopharynx. At the completion of feeding, prey were pushed off the hypopharynx with the foretarsi while the asilid was still at the feeding site or prey were dropped in flight as the asilid resumed foraging.

The numbers, sizes and percentages of prey of different taxon taken by *E. cressoni* in Wyoming are given in Table 2 and show that Diptera (Fig. 2) constituted 72 percent of the number of prey taken. Lavigne and Dennis (1985) indicate that *E. cressoni* in Mexico fed primarily on Diptera and Homoptera and that these two orders comprised ca. 66 percent of the prey. Presumably differences in prey selection for the two populations are due primarily to availability of prey. As previously indicated, *E. cressoni*'s habitat in Wyoming was near a reservoir and



Figs. 1-2. 1, Rock-studded hillside habitat of *Efferia cressoni* in Guernsey State Park, Guernsey, Wyoming. 2, *Efferia cressoni* male in Wyoming with unidentified Diptera as prey.

this probably contributed to opportunistic predation on Chironomidae which comprise approximately 72 percent of the Diptera prey.

Differences in prey selection between *E. cressoni* in Wyoming (Table 3) and Mexico (Lavigne and Dennis, 1985) are also reflected in the predator to prey ratios. In Wyoming, both sexes fed on smaller prey than was observed for the population in Mexico, as indicated by the larger mean ratio of predator to prey.

Overall *E. cressoni* in Wyoming and Mexico were 3.8 and 2.6 times as large as their prey, respectively. This difference is not surprising since prey size of asilids varies with the taxon of the prey.

The following is a list of prey taken by *E. cressoni* in Wyoming. Lavigne and Dennis (1985) list this species' prey for the population studied in Mexico. COLEOPTERA, Dasytidae: unidentified, VI-11-78 (2 ♀), VI-15-78 (♀), VI-16-78 (4 ♀); Nitidulidae: *Carpophilus pallipennis* (Say), VI-16-78 (♂), VI-18-78 (2 ♂); DIP-TERA, Anthomyiidae: unidentified, VI-15-78 (♂); Asilidae: *Efferia cressoni* (Hine), VI-11-78 (♀); *Holopogon seniculus* Loew, VI-16-78 (2 ♀), VI-18-78 (♀); Cecidomyiidae: unidentified, VI-16-78 (♂), VI-18-78 (♀); Chironomidae: unidentified, VI-7-78 (♂), VI-11-78 (7 ♂, 10 ♀), VI-14-78 (2 ♂, 4 ♀), VI-15-78 (♂, 4 ♀), VI-16-78 (5 ♂, 27 ♀), VI-18-78 (2 ♂, 10 ♀); Chloropidae: *Hippelates* sp. prob. *pusio* Loew, VI-16-78 (♀); *Meromyza* sp., VI-18-78 (♀); Phoridae: unidentified, VI-16-78 (♀); Pipunculidae: unidentified, VI-16-78 (♂, ♀); Sciaridae: unidentified, VI-16-78 (2 ♀), VI-18-78 (2 ♀); Simuliidae: unidentified, VI-16-78 (2 ♀), VI-18-78 (♀); Tachinidae: unidentified, VI-7-78 (♀), VI-15-78 (♂, ♀), VI-16-78 (2 ♀); unidentified, VI-16-78 (3 ♀), VI-18-78 (♀); HEMIPTERA, Lygaeidae: *Nysius* sp., VI-14-78 (♀); Miridae: unidentified, VI-15-78 (♂), VI-16-78 (♂, 2 ♀); HOMOPTERA, Aphididae: unidentified winged adult, VI-14-78 (♀); Cicadellidae: *Aceratagallia* sp., VI-14-78 (♀); *Aceratagallia uhleri* (Van Duzee), VI-14-78 (♂); *Athysanella* sp., VI-16-78 (♀); *Cuerna* sp., VI-14-78 (♀), VI-15-78 (♀); *Flexamia flexulosa* (Ball), VI-11-78 (♀), VI-14-78 (♀); *Flexamia* sp., VI-16-78 (♀); unidentified, VI-11-78 (♀), VI-14-78 (2 ♀); nymph, VI-15-78 (♂), VI-16-78 (♀), VI-18-78 (♀); Issidae: *Bruchomorpha beameri* Doering, VI-14-78 (♀); HYMENOPTERA, Ichneumonidae: Chalcidoidea, VI-15-78 (♀), VI-16-78 (♂, 3 ♀); LEPIDOPTERA, unidentified: VI-11-78 (♀), VI-14-78 (♀), VI-15-78 (♀); ORTHOPTERA, unidentified: nymph, VI-11-78 (♀).

In both Wyoming and Mexico *E. cressoni* exhibited cannibalism. In Wyoming, this species also was observed two times to be preyed on by jumping spiders (Salticidae). One of the spiders was identified as *Pellenes* sp., *viridis* group.

Mating behavior. — Male *Efferia cressoni* in Mexico have been observed making searching flights for receptive females with which to mate. However, this behavior was not observed in Wyoming.

Matings were initiated in flight when the male grasped the female on the dorsum of her thorax and the struggling pair fell to the ground. The male then clasped the female's genitalia and the pair typically flew onto vegetation.

During mating *E. cressoni* remain in the male-over-female position (Fig. 3). In this position the male's abdomen curved around to the right or left of the female's abdomen and clasped her genitalia from below. The male's and female's wings were generally spread at a 30 to 45 degree angle to their bodies (some males folded their wings over their dorsum). *Efferia cressoni* males in Mexico rested their foretarsi on the female's eyes; males in Wyoming also rested their foretarsi on the dorsum of the female's thorax.

In Mexico, two complete matings for this species were 7 and 7.5 min. Partial copulation times for *E. cressoni* in Wyoming ranged from 1 to 10 min., but only one complete mating was observed to last 5.5 min. As mating neared completion, males frequently briefly buzzed their wings. Then, just before termination, males buzzed their wings again, moved to the female's side and pushed off with all six

Table 1. Comparative ethology of eighteen species of *Efferia*.¹

	<i>E. aestuans</i>	<i>E. albi- barbis</i>	<i>E. argyro- gaster</i>	<i>E. benedicti</i>	<i>E. bicau- data</i>	<i>E. cressoni (Mex)</i>	<i>E. cressoni (Wyo)</i>	<i>E. frewingi</i>
Foraging Sites								
From soil	X		X	X	X	X	X	X
From vegetation	X		X	X	X	X	X	X
Prey Capture Methods								
On soil								X
On vegetation								
In air			X	X	X	X	X	X
Immobilization of Prey								
In air			X	X	X	X	X	X
At feeding site								X
Prey Manipulation Methods								
Hovers in air—all legs			X	X	X	X	X	X
On soil—crawls on prey								
On soil—combination of legs								
Prey Specificity								
Stenophagic							X	
Euryphagic	X	X	X	X		X		X
Cannibalism Observed								
				X		X	X	X
Courtship Behavior of Males								
None observed			X				X	
Searching flights				X		X		X
Buzzes wings in flight								
Copulatory Position								
Male over female			X	X	X	X	X	X
Behavior During Copulation								
Pair quiet unless dis- turbed								
Male intermittent wing buzz						X	X	X
Male terminal wing buzz			X			X	X	X
Male strokes female's abdomen			X					X
Male moves female's head with foretarsi				X				
Pair moves from ground to vegetation			X					X
Male falls off to side at termination of mat- ing						X	X	
Duration of Copulations								
Range in minutes			6-7.5			7-7.5		6-24
Average in minutes			6.75	1.75		7.25	5.5	14.9

Table 1. Extended.

<i>E. helenae</i>	<i>E. interrupta</i>	<i>E. kondratieffi</i>	<i>E. nemoralis</i>	<i>E. pallidula</i>	<i>E. pogonias</i>	<i>E. rapax</i>	<i>E. staminea</i>	<i>E. subcuprea</i>	<i>E. triton</i>	<i>E. varipes</i>
X				X	X		X	X	X	X
X		X	X	X	X		X	X	X	X
										X
X				X			X	X	X	X
X				X			X	X X	X	X
X				X			X	X	X	X X
								X	X	X
										X
X	X			X		X	X	X	X	
X		X		X			X			
X				X			X		X	X
									X	
X				X			X	X	X	X
				X						
								X	X	
X							X		X	X
X							X	X		
	X									
X										X
								X	X	
4-12 7.6				1.5			3	6.5 6.5	0.75-1.5 1.0	11.5-14 12.76

Table 1. Continued.¹

	<i>E. aestuans</i>	<i>E. albibarbis</i>	<i>E. argyro-gaster</i>	<i>E. benedicti</i>	<i>E. bicaudata</i>	<i>E. cressoni</i> (Mex)	<i>E. cressoni</i> (Wyo)	<i>E. frewingi</i>
Oviposition Sites								
In or on vegetation	X		X	X		X	X	
In soil		?						X
Duration of Ovipositions								
Range in minutes			0.5–1.5	2.5–3		0.75–1.0		0.9–2
Average in minutes						0.88		1.7
Number of Eggs/Clutch	1–90		2–19			2–5		3–7
Average Egg Measurements (mm)								
Length	0.8		1.2			1.41		1.63
Width	0.25		0.4			0.54		0.72

¹ The behavioral data for the genus is compiled from the authors' observations and the following published sources: Baker and Fischer, 1975 [*E. aestuans* (Linnaeus)]; Bromley, 1914 [*E. aestuans*, *E. rapax* (Osten Sacken)], 1930 [*E. interrupta* (Macquart), *E. rapax*], 1942 [*E. aestuans*], 1945 [*E. aestuans*, *E. albibarbis* (Macquart), *E. interrupta*, *E. rapax*], 1946a [*E. aestuans*, *E. interrupta*, *E. rapax*], 1946b [*E. aestuans*, *E. rapax*], 1948a [*E. aestuans*], 1948b [*E. aestuans*, *E. albibarbis*, *E. rapax*], 1950 [*E. aestuans*, *E. albibarbis*, *E. interrupta*, *E. rapax*]; Bullington and Lavigne, 1984 [*E. kondratieffi* Bullington and Lavigne]; Dennis and Lavigne, 1976, [*E. varipes* (Williston)]; Fattig, 1945 [*E. aestuans*, *E. albibarbis*, *E. femorata* (Macquart), *E. rapax*]; Hull, 1942 [*E. interrupta*]; Lavigne, 1964 [*E. helenae* (Bromley)], 1972 [*E. bicaudata* (Hine), *E. helenae*], 1979 [*E. argyrogaster* (Macquart)]; Lavigne and Dennis, 1975 [*E. frewingi* Wilcox], 1985 [*E. cressoni* (Hine), *E. subcuprea* (Schaeffer), *E. triton* (Osten Sacken)]; Lavigne et al., 1976 [*E. benedicti* (Bromley)], 1980 [*E. frewingi*]; Lavigne and Holland, 1969 [*E. helenae*, *E. pallidula* (Hine), *E. staminea* (Williston)]; Lavigne and Pfadt, 1966 [*E. bicaudata*, *E. helenae*, *E. pallidula*, *E. staminea*]; Linsley, 1960 [*E. interrupta*, *E. rapax*]; McAtee and Banks, 1920 [*E. aestuans*, *E. albibarbis*, *E. nemoralis* (Hine)]; Painter, 1926 [*E. albibarbis*]; Reinhard, 1938 [*E. aestuans*]; Rogers and Lavigne, 1972 [*E. bicaudata*, *E. helenae*, *E. pallidula*, *E. staminea*, *E. varipes*]; Scarbrough, 1972 [*E. aestuans*, *E. interrupta*], 1974 [*E. aestuans*, *E. pogonias* (Wiedemann)].

legs (Fig. 4). Some male *E. cressoni* in Wyoming also have been observed to vigorously pump their genitalia up and down towards the end of mating. This behavior was not reported by Lavigne and Dennis (1985) for males in Mexico.

Temperatures at the heights (5 cm to 1 m above the ground) of copulating pairs of *E. cressoni* on vegetation ranged from 25–40°C in Wyoming; those in Mexico were 27.2 and 29.4°C.

Oviposition behavior.—Female *E. cressoni* oviposited in grass seed heads, and between the sheath and stem of grass stalks (Fig. 5). Temperatures taken at heights (10–12 cm) of *E. cressoni* ovipositions in Wyoming ranged from 29.4–37.8°C, those in Mexico at 33–34°C.

Eggs have not been collected for *E. cressoni* in Wyoming, but in Mexico females deposited 2 to 5 eggs per oviposition. These eggs had an average length and width of 1.41 and 0.54 mm, respectively.

Daily rhythm of activity.—A comparison of the daily rhythm of activity of *E. cressoni* in Wyoming and at Rancho Experimental "La Campana," shows that at the latter site this species exhibited more distinct, shorter periods of mating and oviposition behavior throughout the day. In Wyoming, *E. cressoni* had less distinct, longer periods of mating, oviposition and foraging behavior (Fig. 6). This relatively constant level of behaviors, may in part be due to the relatively rapid

Table 1. Extended.

<i>E. helenae</i>	<i>E. inter-rupta</i>	<i>E. kondra-tiefti</i>	<i>E. nemo-ralis</i>	<i>E. pallidula</i>	<i>E. pogo-nias</i>	<i>E. rapax</i>	<i>E. staminea</i>	<i>E. sub-cuprea</i>	<i>E. triton</i>	<i>E. varipes</i>
X	?			X X		?	X	?	X	X
0.5-1.5									0.6-2	0.5-3
0.75									1.23	1.75
1-7				1-15			2-10		3-13	10-40
1.31				1.09			1.30		1.72	1.28
0.48				0.41			0.36		0.58	0.41

changing weather in Wyoming during the summer and the need by flies to take advantage of good weather.

COMPARATIVE ETHOLOGY OF *EFFERIA*

Foraging and feeding behavior.—All species of *Efferia* studied to date forage from both the ground (soil, rocks, twigs, etc.) and vegetation, depending on the soil surface temperature. Foraging from the ground takes place until the surface temperature reaches 40 to 49°C. Above this range of temperatures, *Efferia* move onto vegetation to forage. One species, *E. subcuprea*, forages primarily from vegetation at heights of 1 to 2 m and rarely ventures to the ground. *Efferia aestuans* also forage mainly from vegetation and only occasionally from the ground.

Efferia exhibit other adaptations to temperature fluctuations. During cooler parts of the day they frequently flatten themselves against the ground, with their bodies broadside to the sun. When ground temperatures approach the point where the asilids begin to move onto vegetation, they assume various postures, such as holding their bodies high off the substrate and facing the sun. Additionally, *E. triton* has been observed to hold its foretarsi over its head at high ground temperatures. While on vegetation *Efferia* frequently move into the shade of rocks and vegetation. Similar adjustments to temperature have been observed for other species of Asilidae. These adjustments allow the robber flies to function in areas of optimal temperature.

As *Efferia* forage, they often face into the sun, thus backlighting potential prey objects and presumably making them more easily discerned. In addition, some species (e.g. *E. varipes*) rest with their bodies at a 40 to 45 degree angle to the substrate. Since the central ommatidia of an asilid's eye have greater powers of vision than do the outer ones (Melin, 1923), this posture probably also allows the asilids to see prey more clearly. As they rest at ground level or on vegetation, *Efferia* move their heads more frequently than their bodies.

Efferia often chase potential prey or make investigatory flights while foraging. They also capture and release potential prey if they cannot insert their hypopharynx or find the prey unsuitable because of some other characteristics.

Table 2. Numbers and percentages of prey of different taxa captured by males and females of *Efferia cressoni* in Wyoming.

Taxa	Males				Females			
	No.	%	Range (mm)	$\bar{x}$	No.	%	Range (mm)	$\bar{x}$
Coleoptera	1	3.6	3.2	3.2	9	7.8	2.8–3.6	3.2
Diptera	22	78.6	1.6–5.7	3.6	81	70.4	1.0–13.5	3.1
Hemiptera	2	7.1	2.1–2.8	2.5	3	2.6	2.7–6.5	4.2
Homoptera	2	7.1	2.5–3.4	3.0	14	12.2	2.3–8.0	4.5
Hymenoptera	1	3.6	2.6	2.6	4	3.5	0.8–2.7	1.5
Lepidoptera	—	—	—	—	3	2.6	5.9–6.5	6.2
Orthoptera	—	—	—	—	1	0.9	0.9	0.9
Total	28	100	1.6–5.7	3.5	115	100	0.8–13.5	3.3

While the forage flights of most *Efferia* cover distances up to 5 m, prey are usually captured within 1 to 2 m of a foraging site. *Efferia triton* is the only species which has been observed to capture prey at the same mean distances it forages. Lavigne and Dennis (1985) suggest that this species may have better vision than other *Efferia* species.

Prey are usually captured in the air. However, three species (*E. frewingi*, *E. triton* and *E. varipes*) have been reported occasionally to capture prey on soil or vegetation.

Once prey are captured *Efferia* usually insert the hypopharynx into the prey prior to landing to feed, often times while hovering above the site. Additionally, *Efferia frewingi* and *E. subcuprea* occasionally immobilize prey on the ground, presumably because of the prey's large size or because of the difficulty encountered in subduing the prey.

During feeding the most common method of repositioning prey prior to reinserting the hypopharynx, is hovering above the feeding site and manipulating the prey with all six tarsi. *Efferia subcuprea*, *E. triton* and *E. varipes* also manipulate prey with a combination of legs while resting on the soil, and *E. varipes* may crawl over its prey before reinserting its hypopharynx. These latter two methods appear to be utilized when the prey is too large to be manipulated during a hover flight. Other members of the subfamily Asilinae to which *Efferia* belongs, also commonly hover while manipulating prey.

Upon completion of feeding prey are usually, (1) pushed off the asilid's hypopharynx with the foretarsomeres while the asilid is still on the feeding site, or (2) dropped in flight as the asilid moves to a new location and/or resumes foraging.

With the exception of *E. varipes* and *E. cressoni* in Wyoming, the *Efferia* studied

Table 3. Comparison between length of *Efferia cressoni* and that of its prey in Wyoming.

Sex	Predator Length (mm)*			Prey Length (mm)			No. of Prey Measured	Mean Ratio of Predator to Prey
	Minimum	Maximum	Mean	Minimum	Maximum	Mean		
Male	10.5	14.0	12.3	1.6	5.7	3.5	28	3.5
Female	11.3	16.0	13.6	0.8	13.5	3.3	115	4.1
Species Mean			12.9			3.4		3.8

* 10 predators of each sex were measured.



Figs. 3–4. 3, *Efferia cressoni* pair in copula on plant stem in Wyoming. 4, *Efferia cressoni* male in first phase of separation from female in Wyoming.

to date appear to be fairly non-selective in their choice of prey (i.e. euryphagic—no one insect order makes up more than 50 percent of the prey). In the case of *E. varipes*, Orthoptera made up 52 percent of its prey (Dennis and Lavigne, 1976), while Diptera served as 72 percent of the prey of *E. cressoni* in Wyoming. For several other species, one or two orders (usually Diptera, Homoptera and/or Hymenoptera) may represent 30 to 40 percent of the prey taken.

Cannibalism is practiced by most *Efferia* species. Members of the genus can serve as prey for other species of Asilidae, including other *Efferia*. As previously



Fig. 5. *Efferia cressoni* female ovipositing in Wyoming.

indicated, jumping spiders (Salticidae) have been observed preying on *E. cressoni* in Wyoming. Mites also have been observed attached to various parts of bodies of *E. frewingi*.

Mating behavior.—Prior to the initiation of mating, most *Efferia* males, for which there is adequate data, exhibit searching flights for receptive females. These flights usually consist of males weaving in-and-out of vegetation looking for females. Additionally, *E. triton* males buzz their wings during these flights, thus providing a possible auditory stimulus.

Most matings are initiated in flight when the male overtakes the female and the struggling pair falls to the ground where mating ensues in the male-over-female position. *Efferia benedicti*, *E. helenae*, *E. staminea* are the only species which have been observed to initiate mating on the ground or vegetation.

While in the male-over-female position, the male's abdomen curves around to the right or left of the female's abdomen and clasps her genitalia from below. The male's and female's wings are generally spread at a 30 to 45 degree angle to their bodies, although some males may fold their wings over their bodies. The male's foretarsi typically rest on the female's eyes.

During copulation some *Efferia* (e.g. *E. cressoni*) move from the soil surface to vegetation. Males of most species studied exhibited wing buzzing during mating (especially a terminal buzz) or stimulatory behavior using the fore or hind tarsi. When these behaviors occur towards the end of copulation, they may also signal to the female that the end of mating is imminent. As previously indicated, some male *E. cressoni* in Wyoming also have been observed to vigorously pump their genitalia up and down towards the end of mating.

Most *Efferia* mate for about 6 to 14 min. *Efferia bicaudata*, *E. pallidula*, *E. staminea* and *E. triton* mate for less than 3 min.; whereas, *E. frewingi* may mate for as long as 24 min.

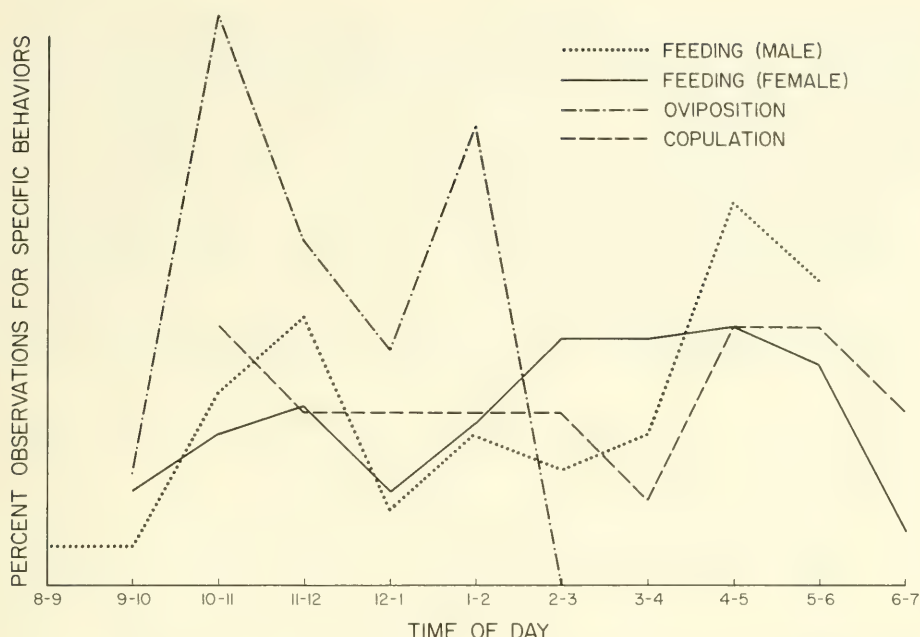


Fig. 6. The diurnal rhythm of activity of *Efferia cressoni* in Wyoming. (The percentage of asilids engaged in specific behavior patterns was calculated from the total number of observations of each behavior—45, 146, 20, 15—for male feeding, female feeding, mating and oviposition, respectively.)

Efferia typically terminate mating when the male does one or more of the following, (1) falls to one side of the female and pushes off using all tarsomeres (e.g. *E. cressoni*, Fig. 4), (2) crawls up on the female's dorsum and pushes off, (3) rises into the air and flutters his wings while releasing his claspers (only *E. benedicti*), and (4) pushes off of the female without falling to one side, crawling up on the female's dorsum or rising into the air.

Oviposition behavior.—The site of egg deposition depends primarily on the shape of the female's ovipositor. Females with cylindrical ovipositors (i.e. *E. frewingi* and *E. helenae*) deposit eggs in the soil, while females with laterally flattened ovipositors deposit eggs in or on vegetation (e.g. *E. cressoni* in Wyoming). *Efferia pallidula* is the only species that has been observed to oviposit in both soil and vegetation; its ovipositor is laterally flattened.

Individual ovipositions take from 0.5 to 3 min., during which generally 2 to 19 eggs are laid. *Efferia varipes* and *E. aestuans* are the only species reported to deposit more than 19 eggs/clutch. For those species which can be followed by the investigator for extended periods of time, multiple ovipositions can usually be observed.

All collected *Efferia* eggs are oval-oblong and creamy-white. Average widths range from 0.25 to 0.72 mm; average lengths range from 0.8 to 1.72 mm.

Daily rhythm of activity.—Some detailed information on daily activity pattern has been reported for five species of *Efferia*: *cressoni*, *subcuprea*, and *triton* in Mexico (Lavigne and Dennis, 1985), and *frewingi* (Lavigne and Dennis, 1975) and *varipes* (Dennis and Lavigne, 1976) in Wyoming. That of *E. cressoni* in

Wyoming was discussed previously in this paper. All six of these species forage throughout the day with one or two peak periods of activity. These peaks are often slightly more pronounced than the remaining time periods. However, mating and/or oviposition behavior are generally restricted to one or two time periods of the day. For example, in Wyoming the majority of ovipositions by *E. cressoni* females takes place between 1000 and 1500 h (Fig. 6).

As the percentage of asilids engaged in one particular behavior increases, the percentage engaged in other behaviors decreases (e.g. in Wyoming female *E. cressoni* foraging activity is least during the midday period and greatest during late afternoon from 1500 to 1700 h). Additionally, temperature may be important in determining the occurrence of different behaviors throughout the day.

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NEW SPECIES OF TORTRICID MOTHS FROM EASTERN
NORTH AMERICA (LEPIDOPTERA: TORTRICIDAE)

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Abstract.—*Sparganothis lamberti*, *Lozotaenia costinotana*, *Lozotaenia exomilana*, and *Archips nigriplagana*, four new species of Tortricidae, are described from eastern North America.

When I gave my collection of microlepidoptera to the United States National Museum of Natural History a few years ago, there were among the undescribed species four species of tortricids for which I had prepared descriptions. At that time no species of *Lozotaenia* in its correct sense had been recorded from North America, and until now none has been recorded from eastern North America. Recently I was asked by J. F. Gates Clarke to publish the description of the *Sparganothis* species; we decided that it was advisable that all four species be described so all the specimens of the species could be released to the collection.

Sparganothis lamberti Franclemont, NEW SPECIES

Figs. 1, 2, 8, 9

A moderate-sized, very brilliantly colored and distinctive appearing tortricine; superficially it shows a vague resemblance to *S. irrorea* (Robinson), but it lacks any evidence of the transverse striae of that species. The genitalia associate the species with *S. pettitana* (Robinson) from which it differs in both pattern and wing texture.

Description: Male.—Costal fold of fore wing short, only slightly more than one-ninth length of costa. Inner margin of hind wing modified to form a pocket containing a hair pencil. Palpi, head, collar (patagia), and bases of tegulae dark, glistening brown with some iridescent reflections; disc of thorax and apical halves of tegulae bright golden yellow. Fore and middle legs deep brown on outer sides, inner sides golden white. Fore wing with ground color clear, bright, golden yellow, concolorous with disc of thorax; no striae nor reticulate markings; costal fold dark, shining brown, concolorous with head and collar, followed by triangular costal spot of same color; large quadrate brown patch, beginning just beyond middle of inner margin, extending half-way to outer angle, and extending costad to lower margin of discal cell; dark brown, punctiform spot at end of cell above outer part of dark patch; dark brown subterminal band, well marked toward costa, evanescent below middle of wing; broad marginal band of golden brown scales; pale golden brown shade from subterminal band to quadrate patch, upper boundary diagonal from below apex to quadrate patch, covering outer fourth of wing; fringe dark; a few dark brown scales on inner margin at base. Hind wing uniformly

pale golden brown; dorsum of abdomen concolorous. Beneath, fore wing golden brown, paler along costa; hind wing paler golden brown; venter of abdomen pale, concolorous with hind wing.

Female.—Palpi, head, collar, and bases of tegulae as in male, glistening dark brown; disc of thorax and apical halves of tegulae deep golden yellow. Legs as in male. Fore wing ground color deep golden yellow; base of costal margin dark brown; dark, triangular costal spot of male absent; dark quadrate patch along inner margin and dark subterminal area obscured in dark golden brown shade, upper margin diagonal from just before apex to middle of inner margin; some dark transverse striae in shaded area; dark punctiform spot about one-third from base, second such spot, in most specimens, at end of discal cell, in same position as that in male. Hind wing uniformly golden brown; dorsum of abdomen concolorous. Beneath as in male.

Fore wing length: Male, 19–20 mm, female 21–23 mm.

Male genitalia: Fig. 1; similar to *pettitana*, but slightly smaller and with spiculate area on transtilla broader and more rounded.

Female genitalia: Fig. 2.

Holotype ♂. Cherry Hill Recreation Area, Route 107, 2000 ft., Oconee County, South Carolina, 22 August 1958; J. Franclemont. Genitalia slide JGF 4073. United States National Museum of Natural History collection.

Paratypes: 54 ♂, 50 ♀. 48 ♂ and 48 ♀, same locality as holotype, 7 August to 7 September 1958; 6 ♂, 2 ♀, Highlands 3865 ft., Macon County, North Carolina, 19 July to 24 August 1958, J. G. Franclemont. Most in the collection of the United States National Museum of Natural History.

In addition to the type series the species has been seen from Louisiana, four males taken by V. A. Brou 4.2 miles NE of Abita Springs, St. Tammany Parish.

This species is dedicated to the late Robert Lambert who completed a preliminary revision of the genus *Sparganothis* for his doctoral dissertation at Cornell University.

Lozotaenia costinotana Franclemont, NEW SPECIES

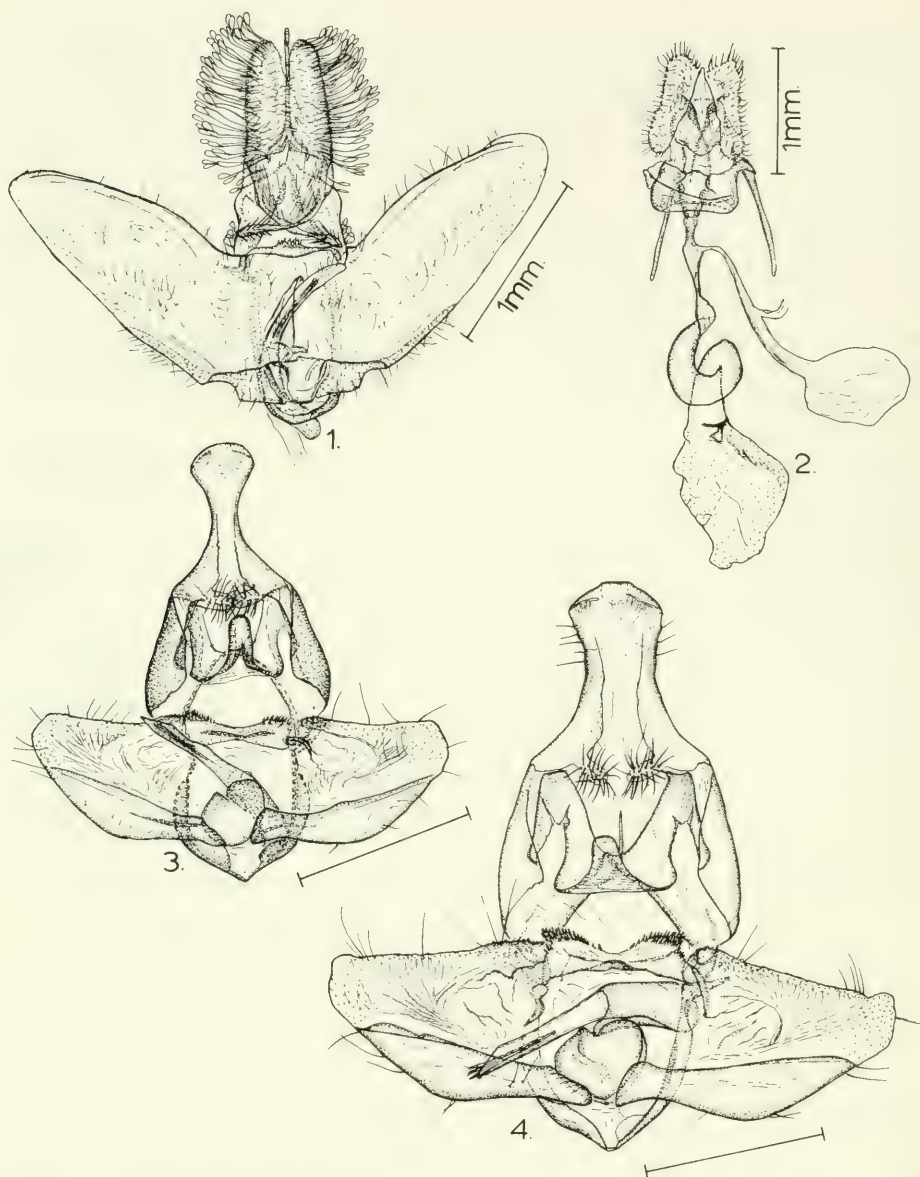
Figs. 3, 13

A species of moderate size with a wing expanse of 19 mm, it differs from both *exomilana* Franclemont and *hesperia* Powell (1962, p. 841) by its smaller size and pattern. It appears most like *rindgei* Obraztsov (1962, p. 17) in pattern, but it is readily distinguished by the male genitalia; *rindgei* has a broad, parallel-sided uncus with a more or less truncate apex, a striking contrast to the spoon-shaped uncus of *costinotana*.

Description: Palpi, head, and thorax gray brown; tegulae pale tipped. Legs fuscous brown on outer sides, whitish on inner sides. Fore wing gray white, whitest along costa and outer margin; disc slightly infusate, darker toward base; pattern of closely spaced, narrow, irregular, blackish-brown transverse lines, giving a somewhat reticulate appearance; black, subquadrate costal spot at basal third of wing; a smaller somewhat similar spot, but with some white scales centrally, at outer fourth. Hind wing white, slightly infusate; inner margin and apical area with brownish-black scales. Abdomen whitish above, fuscous brown below.

Fore wing length: 9.5 mm.

Male genitalia: Fig. 3.



Figs. 1-4. *Sparganothis lamberti*. 1, Male genitalia. 2, Female genitalia. 3, *Lozotaenia costinotana*, male genitalia. 4, *Lozotaenia exomilana*, male genitalia.

Holotype ♂. Passadumkeag, Penobscot County, Maine, 30 June 1956; J. G. Franclemont. Genitalia slide JGF 4474. United States National Museum of Natural History collection.

***Lozotaenia exomilana* Franclemont, NEW SPECIES**

Figs. 6, 7, 12

A moderately large tortricine with a wing expanse of 23 to 26 mm that is very similar to *forsterana* (Fabricius) of Europe, but with white scales along the costal

area and the outer margin, and with a conspicuous median shade on the fore wing. The male genitalia differ from those of *forsterana* by the more massive uncus and the shape of the valves; from the somewhat similar *hesperia* they differ in the same characters and in the same way. The elongate, yellowish hair-pencil in a groove between the procoxa and the mesocoxa that was mentioned in the description of *hesperia* is present in *exomilana*; it is apparently absent in *costinotana*.

Description: Palpi, head, and thorax deep fuscous brown. Legs dark fuscous brown on outer sides, grayish white on inner sides. Fore wing pale gray brown with considerable amount of white along costa and outer fourth of wing, giving a silvery appearance; pattern of closely spaced, fine irregular, brownish-black transverse lines, giving a somewhat reticulate appearance; conspicuous, subquadrate black spot at basal third of costa, a triangular black spot at outer fourth of costa; prominent blackish-brown shade from below outer angle of basal costal spot to inner margin, reaching from outer two-thirds to almost outer angle. Hind wing pale fuscous gray, darker at apex and along outer and inner margins. Abdomen above grayish white, below dark fuscous brown.

Expanse of fore wing: 11–13 mm.

Male genitalia: Fig. 4.

Female genitalia: Fig. 5.

Holotype ♂. Highlands 3865 ft., Macon County, North Carolina, 11 July 1958; J. G. Franclemont. Genitalia slide JGF 4473. United States National Museum of Natural History collection.

Paratypes: 2 ♂: same locality as holotype, 24 June 1958, and 11 July 1958; 1 ♀: same locality as holotype, 1 July 1958; J. G. Franclemont. United States National Museum of Natural History collection.

One of the paratypes, the male taken on 11 July, shows a large amount of brownish suffusion on the fore wings, thus obscuring most of the other markings.

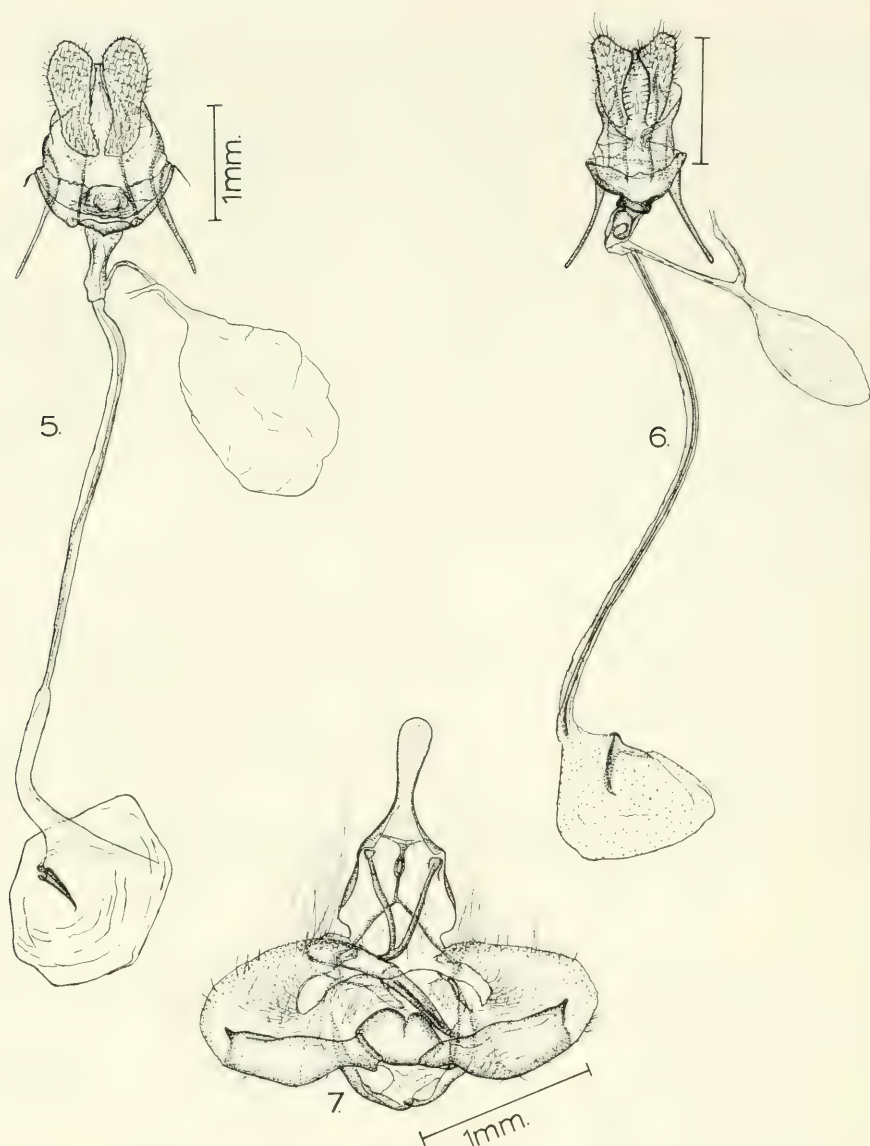
Archips nigriplagana Franclemont, NEW SPECIES

Figs. 6, 7, 10, 11

A very distinctive appearing species of moderate size, the male has a wing expanse of 19 mm and the female 23 mm; the species is perhaps suggestive of *Choristoneura fractivittana* (Clemens), but it is closely related to *Archips arhyrospila* (Walker) by the characters of the male and the female genitalia. The females differ from those of *arygrospila* by the slightly excavated costal and outer margins of the fore wing, agreeing in these characters with *Archips mortuana* Kearfott.

Although the specimens are from two widely separated areas, New York and North Carolina-Kentucky, the specimens from North Carolina and New York were collected in similar habitats, acid soil areas in the Upper Transition Zone. It is the widely separated localities where the moths have been taken that have suggested that we may be concerned with a discrete species.

Description: Male.—Costal fold well developed, extending one-third length of costa of fore wing. Head, thorax, and ground color of fore wing yellow tawny; fore wing with some narrow, irregular, darker transverse bands and two small dark spots in basal area; wide, black band from center of costa, outwardly oblique, turning abruptly toward outer margin in fold, followed by patch of lead-gray scales reaching almost to outer angle, with some scattered dark scales below fold to inner margin; dark, subtriangular costal spot at outer fourth; subterminal area without evident markings; fringe concolorous with ground. Hind wing light gray on base



Figs. 5-7. 5, *Lozotaenia exomilana*, female genitalia. *Archips nigriplagana*. 6, Female genitalia. 7, Male genitalia.

and disc; upper half of outer margin and apical margin as well as accompanying fringe light straw color. Beneath pale, with ghost of markings above. Fore and middle legs tawny on outer sides, light straw color on inner sides; hind legs light straw color on both inner and outer sides.

Length of fore wing: 9 mm.

Female.—Similar to male in color and markings, but the darker colors less intense, appearing washed-out; hind wing noticeably paler, darker area smaller in proportion to the total area, pale areas almost white.

Fore wing length: 11 mm.



Figs. 8–13. *Sparganothis lamberti*. 8, Male. 9, Female. *Archips nigriplagana*. 10, Male. 11, Female. 12, *Lozotaenia exomilana*, male. 13, *Lozotaenia costinotana*, male.

Male genitalia: Fig. 7; similar to *argyrospila* but differing in the narrower and longer sclerotized ventral area of the valve. Comparison may be made with the figure in Freeman, 1958 (fig. 16).

Female genitalia: Fig. 6; similar to *argyrospila*, but ovipositor lobes narrowing more toward base; the figure in Freeman, 1958 (fig. 65) may be compared for the differences.

Holotype ♂. McLean Bogs Reserve, Tompkins County, New York, 2 July 1953; J. G. Franclemont. Genitalia slide JGF 4475. United States National Museum of Natural History collection.

Paratypes: 1 ♂ and 3 ♀: Snyder Heights 1100 ft., Ithaca, Tompkins County, New York, 10 July 1979; J. G. Franclemont (♀). Highlands 3865 ft., Macon County, North Carolina, 11 July 1958; J. G. Franclemont (♀). United States National Museum of Natural History collection. Owsley County, Kentucky, 3 miles NE Booneville, 14 June 1980; Loran D. Gibson (♂). Pine Mountain State Park, Kentucky, 6-9-1981 [9 June 1981?]; Carl Cornett (♀). C. V. Covell collection.

The material from Highlands, North Carolina, and from Oconee County, South

Carolina, was collected under the auspices of a Grant, No. 2391 Penrose Fund, from the American Philosophical Society. The summer of 1958 was spent at the Highlands Biological Station where the late Thelma Howell did everything possible to make the summer enjoyable and profitable. Ronald W. Hodges, then a graduate student, was the field assistant that summer. I thank J. F. Gates Clarke and Ronald W. Hodges for reading the paper and for their suggestions. The drawings are by Linda Yu-Ling Chu (Mrs. W. Michael Lai) and the photographs are by the author.

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TAXONOMY OF THE *SEPEDON FUSCIPENNIS* GROUP
(DIPTERA: SCIOMYZIDAE)

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Abstract.—The *Sepedon fuscipennis* group is herein established. A new species, *S. gracilicornis*, and a new subspecies, *S. fuscipennis nobilis*, are described. Included in this group are *S. f. fuscipennis* Loew, *S. floridensis* Steyskal new status, and *S. tenuicornis* Cresson. Illustrations, photos, and maps of the geographic distribution for the group are given.

This study involves the *Sepedon* taxa north of Mexico that lack hairs on the supraspiracular convexity of the metapleuron. These species are here established as the *Sepedon fuscipennis* group, which consists of four species and one subspecies. All are rather large brownish flies similar in size and color to *S. pacifica* Cresson and *S. praemiosa* Giglio-Tos. Adults of the genus all have a striking appearance, with long, porrect antennae and large, grasshopper-like hindlegs.

This paper is concerned with (1) the elevation of the subspecies *Sepedon fuscipennis floridensis* Steyskal to full species rank, (2) recognition of a new subspecies of *Sepedon fuscipennis* Loew, namely *Sepedon f. nobilis*, new subspecies, (3) the separation of *Sepedon gracilicornis*, new species, from *Sepedon tenuicornis* Cresson, (4) illustration of diagnostic characters and distribution maps of all taxa involved, (5) a key to the *Sepedon fuscipennis* group, and (6) a brief summary on recent biological studies.

Because of its large size, widespread distribution and relative abundance, there is more biological data on "*Sepedon fuscipennis*" than any other North American sciomyzid species. Its use for laboratory studies is further enhanced as it is a multivoltine species that overwinters as an adult (Berg et al., 1982). The discovery that sciomyzid larvae prey on aquatic pulmonate snails (Berg, 1953) was based partly on the larvae of this species, collected in marshes in Oakland Co., Michigan, in 1949, and in the Matanuska Valley, Alaska, in 1950-52. The specimens from both of those localities must now be assigned to *Sepedon f. nobilis*.

Biological studies were conducted by Neff and Berg (1966) on both adult and immature stages of *Sepedon fuscipennis*. Their material was obtained from the following widely separated areas: Alberta (Edmonton), Michigan (Cheboygan Co.), New York (Ithaca), and Kentucky (Breckinridge Co.). No geographic variations were noted. However, in light of present findings all but the Kentucky material must be assigned to *Sepedon f. nobilis*.

Population dynamics of adults and larvae of *Sepedon fuscipennis* were studied by Eckblad and Berg (1972). Eckblad (1973) studied the effects of predator and



Fig. 1. *Sepedon f. nobilis*, holotype male, taken before terminal segments were excised and placed in a genitalia vial on the pin beneath specimen. Photo by M. E. Badgley, University of California, Riverside.

prey density, and water depth on the number of snails killed per larva. Arnold (1978) estimated *S. fuscipennis* population density by the capture-recapture method and correlated oviposition rates with temperature and photoperiod at experimental marshes at Cornell University. The effects of temperature on longevity, fecundity, and developmental rates were observed by Barnes (1976). A broad study of phenology and voltinism in the Sciomyzidae (Berg et al., 1982) indicates that *S. fuscipennis* and other species of *Sepedon* are multivoltine and that they overwinter as adults. Berg and Valley (1985) report nuptial feedings in *S. fuscipennis*, with courting males utilizing anal secretions as well as dead snails to attract receptive females. All except the last of these recently published reports are now construed as pertaining to *S. f. nobilis* since the flies observed and tested were from sites in the vicinity of Ithaca, New York, well north of the belt of transition between this taxon and *S. f. fuscipennis*. Personal correspondence with C. O. Berg reveals that the *Sepedon fuscipennis* material in the Berg and Valley (1985) study was collected southwest of the junction of U.S. Rt. 22 and PA Rt. 61, Berks Co., Pennsylvania. The specimens I have seen from that locality collected by K. Valley are "intermediate specimens."

Molluscicide tests were conducted on *Sepedon fuscipennis* by McCoy and Joy (1977) to determine if certain species of marsh flies could survive levels of pesticides that readily kill snails. Being from Green Bottom Swamp, Homestead, Cabell Co., West Virginia, their material probably was *Sepedon f. fuscipennis*.

Extensive biological information is also available on "*Sepedon tenuicornis*,"

though it is less comprehensively studied. In the biological work by Neff and Berg (1966) specimens were taken from three localities in New York: Barrier Corners, Orleans Co.; Benson Ave., Minetto, Oswego Co.; and Inlet Valley, southwest of Ithaca, Tompkins Co. It is likely that the material used was a composite of *Sepedon tenuicornis* and *S. gracilicornis* n. sp. since both species are widely distributed in New York.

An in-depth laboratory study of *Sepedon tenuicornis* was made by Geckler (1971) in regard to (1) number and volume of snails killed per larva, (2) time to first kill, (3) snail vulnerability and larval success. Test specimens were from a small swamp east of Raleigh, North Carolina, and likely were *S. tenuicornis* rather than the more northerly distributed *S. gracilicornis*.

Voucher specimens retained from some of the above studies were made available for the present research. This study re-emphasizes the need in biological and ecological investigations for retention of adequate series of voucher specimens for taxonomic documentation. This problem is further treated by Knutson (1984).

Sepedon is separated from other genera of North American Sciomyzidae north of Mexico by the following combination of characters: (1) propleuron without strong bristle above the base of forecoxa, (2) vellar (subalar) bristles absent, (3) ocellar bristles absent, (4) postocellar bristles well developed, (5) midfemur with one or more distinctly larger anterior setae near midlength of femur, (6) frons with only one fronto-orbital bristle, (7) posterior crossvein arcuate.

Not all species of *Sepedon* have been assigned to groups. Presently recognized are three North American groups—*S. armipes*, *S. pusilla* and *S. fuscipennis*. The *Sepedon armipes* and *S. pusilla* groups, as established by Steyskal (1951), consist of smaller species with wing lengths usually less than 5.4 mm. The *S. armipes* group, which consists of eight species, is uniquely characterized by a deep indentation approximately midway on the ventral surface of the male hindfemur. Females of the *S. armipes* group all have simple hindfemora. Both sexes of the *S. pusilla* group, which consists of five species, have simple hindfemora and in gross aspect are generally darker than the *S. armipes* group. The abdomens are frequently almost black with bluish reflections, while those of *S. armipes* group are brown with little more than a trace of bluish reflection.

Members of the *Sepedon fuscipennis* group are readily separated from all other new world species of *Sepedon* by the absence of hairs on the supraspiracular convexity of the metathorax. In addition, all are relatively large brownish flies with wing lengths between 5.8 mm and 7.4 mm, and the medifacies are without hairs.

KEY TO THE *SEPEDON FUSCIPENNIS* GROUP

- 1. Second antennal segment approximately 2½ times as long as wide in lateral view 2
- Second antennal segment 4 or more times as long as wide in lateral view 4
- 2. Hindtibia with straw colored area in distal half, contrasting with dark brown before and after; male hindtibia with short hairs on dorsal surface. Male genitalia as in Figs. 6, 12 *S. floridensis* Steyskal
- Hindtibia without contrasting area, more or less uniform brown; male hindtibia with hairs as long as width of tibia on dorsal surface 3

3. Frons with distinct velvety black parafrontal spot. Male genitalia as in Figs. 2, 7, 8 *S. f. fuscipennis* Loew
- Frons usually with no more than a trace of a black parafrontal spot in specimens from Canada and western U.S., eastern specimens with darker spot. Male genitalia as in Figs. 3, 9, 10 *S. f. nobilis* new subspecies
4. Second antennal segment approximately 4 times longer than wide, as in Fig. 18. Male genitalia as in Figs. 4, 14 *S. gracilicornis* new species
- Second antennal segment approximately 5 times longer than wide, as in Fig. 17. Male genitalia as in Figs. 5, 13 *S. tenuicornis* Cresson

***Sepedon fuscipennis fuscipennis* Loew**

Figs. 2, 7, 8, 16, 19, 20

This species was described by Loew (1859: 299) and has come to be recognized as the most widely distributed *Sepedon* in North America. However, this study now limits its distribution to mainly southeastern United States. Its western limit is just west of the 100° longitude in southern Texas. The northern limit is just above the 40° latitude in Illinois and Indiana.

The syntype series of this species was examined through the courtesy of Alfred Newton, Museum of Comparative Zoology, Harvard University. The series consists of 1 male and 2 females. Each of the 3 specimens was mounted on a fine pin through the thorax and into a narrow strip of cork near one end. At the opposite end of the cork a much heavier pin was pinned through the cork and bears the specimen information labels. The labels on the pin associated with the male are as follows: (1) a blue label with a "25," (2) a white label with "Loew Coll.," (3) a white label with *fuscipennis* m. [misspelling], (4) a red label with "Type 13228." The females have only the above (2) and (4) labels.

Condition of syntypes.—Male: Wing length 6.2 mm, wings in perfect condition; left hindleg missing; left side of head has eye missing and some of the immediate skeletal material surrounding it; both right and left third antennal segments missing; remainder of specimen in excellent condition. Female #1: Wing length 6.5 mm, wings in perfect condition; extensive anterior damage, rudiments only of a head skeleton, no eyes or face; no propleura or mesopleura; no forelegs. Female #2: Wing length 5.9 mm, wings in perfect condition; left side of face and eye essentially missing; no right foreleg; part of propleura and mesopleura missing.

The terminalia of the male were dissected and the aedeagus is as it appears in Fig. 7. Collection data: Washington [District of Columbia], Osten-Saken. Type no. 13228. Museum of Comparative Zoology. The male is hereby designated as the lectotype.

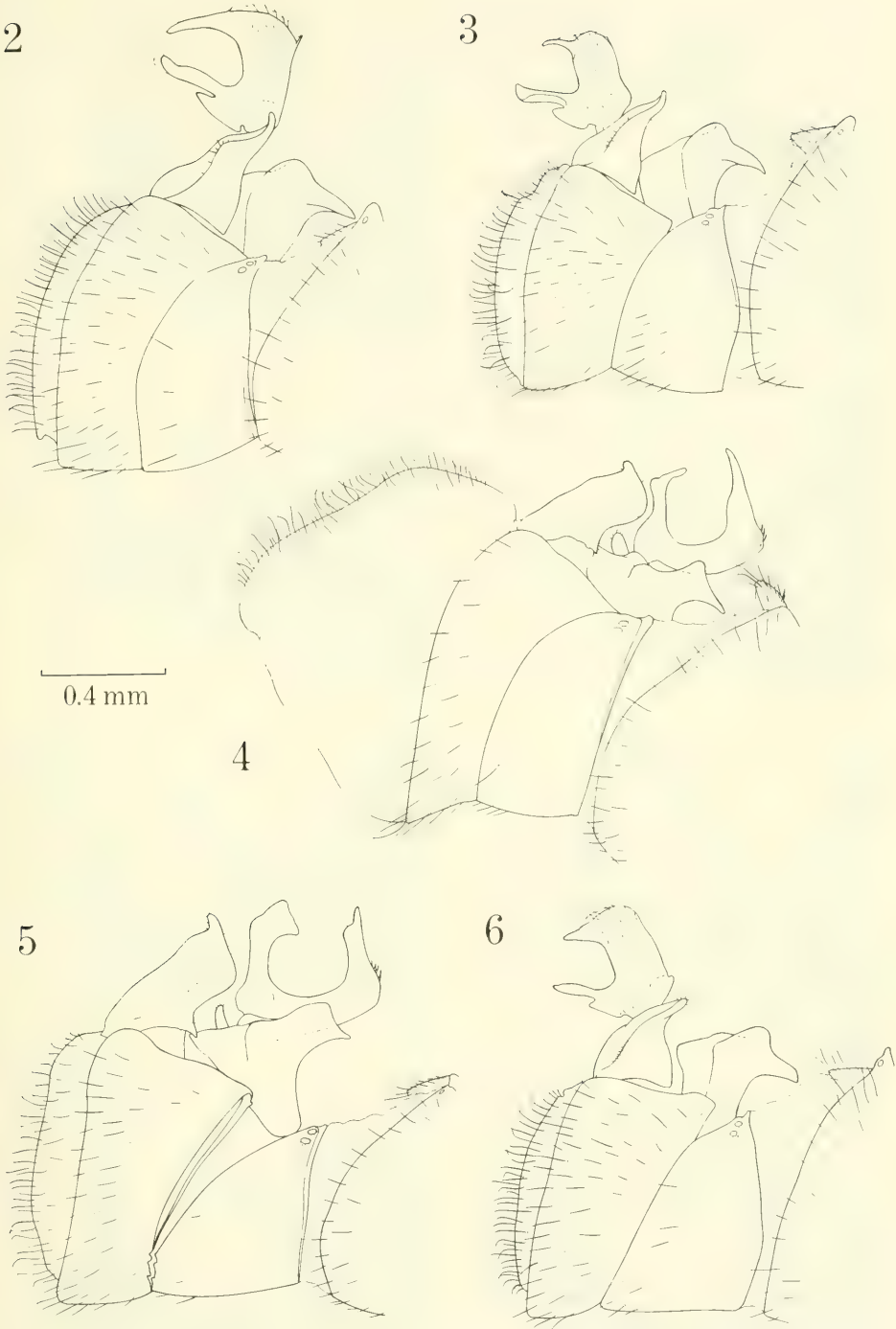
Diagnosis.—Males are separated from *Sepedon f. nobilis* by aedeagal differences. Females are separated by their association with males and with the aid of the distribution map. Both sexes are further distinguished by a dense black parafrontal spot. Diagnostic features of the female terminalia have not been found.

Specimens examined.—415.

***Sepedon floridensis* Steyskal, NEW STATUS**

Figs. 6, 12, 20

It appears justified at this time to elevate *Sepedon fuscipennis floridensis* to full species status. At the time of Steyskal's (1951) description *S. f. floridensis* was known only from a single male from Clewiston, Florida. At that time *S. f. fus-*



Figs. 2-6. Postabdomen, inverted. Sinistral view. 2, *Sepedon f. fuscipennis*, Oxford, Mississippi (CNC). 3, *Sepedon f. nobilis*, paratype, Norman Wells, Northwest Territories (CNC). 4, *Sepedon gracilicornis*, paratype, cercus extended, Hamburg, Livingston Co., Michigan (USNM). 5, *Sepedon tenuicornis*, Edgewater, Maryland (USNM). 6, *Sepedon floridensis*, Grassy Lake, Hempstead Co., Arkansas (USNM).



7



8



9



10



11



12



13



14

cipennis had been reported only as far south as Chatham Co., Georgia, some 350 miles north of Clewiston. At present, the species are sympatric throughout almost their entire range of distribution. I have seen no intergrades between the two species. *Sepedon floridensis* is now known from the following states: Illinois, Tennessee, Kentucky, Maryland, South Carolina, Arkansas, Louisiana and Florida.

The holotype male was examined and agrees well with Figs. 6, 12. Collection data for the holotype: Clewiston, Florida, 20 January 1932, A. L. Melander, National Museum of Natural History, Type no. 101242.

Diagnosis.—*Sepedon floridensis* is easily separated from *S. f. fuscipennis* by comparison of the hind legs (see Figs. 15, 16): (1) the femur of *S. floridensis* is more slender, especially in the proximal one-third; also, the coloration is straw colored proximally, and dark brown distally, whereas *S. f. fuscipennis* is broader and uniformly tawny brown. (2) The tibia of *S. floridensis* has a straw colored area forming a band in the distal half contrasting with dark brown before and after, whereas *S. f. fuscipennis* is tawny brown, sometimes darkened, distally. (3) The hindtibia of *S. floridensis* males have short hairs on the dorsal surface while males of *S. f. fuscipennis* have long hairs. All *S. floridensis* have black parafrontal spots as do *S. f. fuscipennis*; however most western U.S. and Canadian *S. f. nobilis* are without parafrontal spots; at most, they are only lightly marked.

Specimens examined.—80.

***Sepedon fuscipennis nobilis* Orth, NEW SUBSPECIES**

Figs. 1, 3, 9, 10, 20

Holotype male.—Gross aspect brown. Head with broadly excavated frons with weak ridges. Parafrontal spot not present. Second antennal segment slightly more than twice as long as wide. Arista with dense, short, white hairs.

Thorax tomentose, dorsally with 2 longitudinal brown stripes, and 1 lesser median stripe. Prosternum with 2 setae on each side. Pleura brownish with sparsely scattered small setae, except metapleuron and hypopleuron bare. Scutellum with 2 apical bristles only.

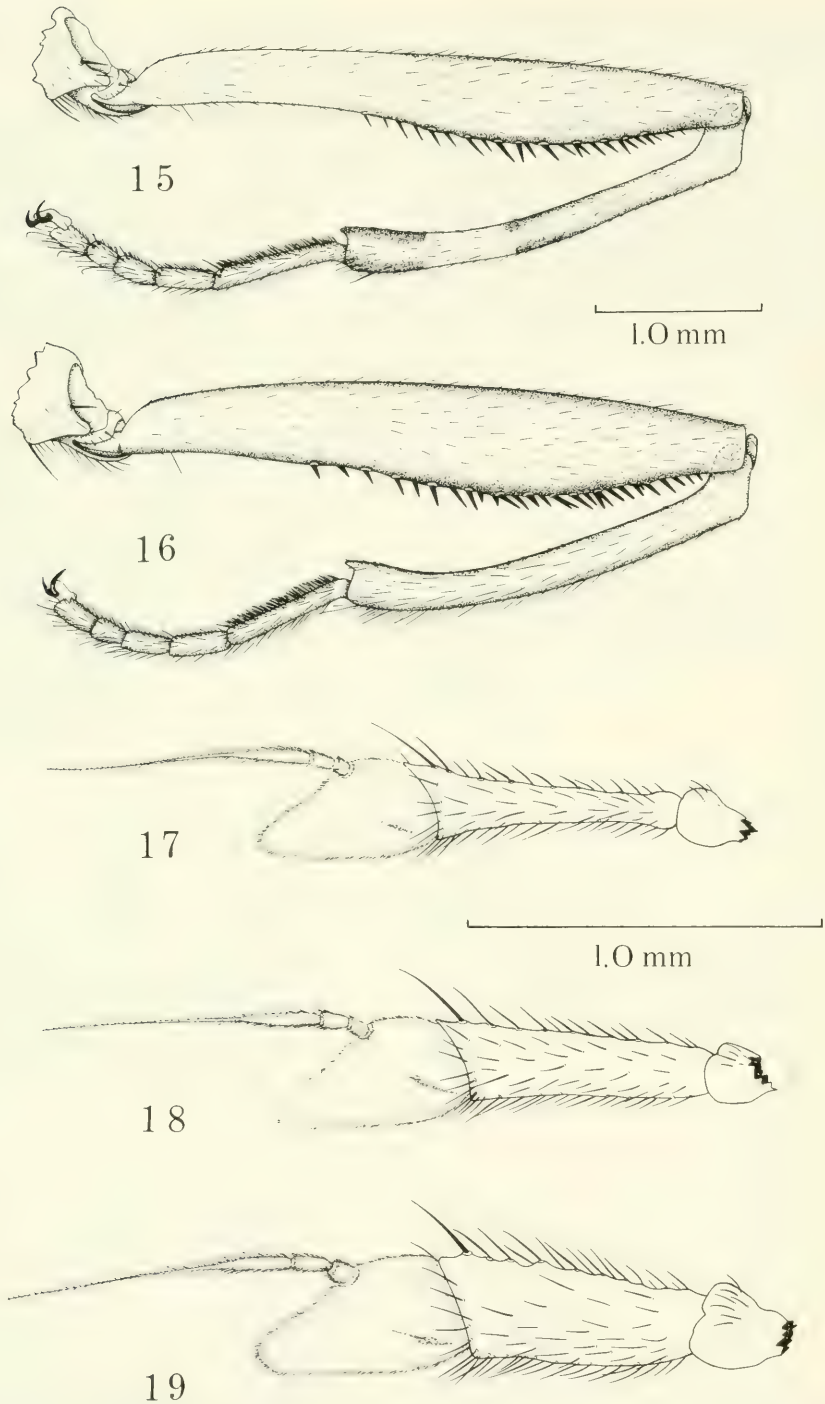
Coxae light brown, tomentose. Legs uniformly brown. Ventral side of hindfemur with double row of heavy spines. Hairs moderately long on dorsal surface of hindtibia.

Wing length 6.7 mm. Membrane brownish, hyaline; costal margin and wing veins brownish. Area around crossveins lightly clouded.

Abdominal segments brownish, darker dorsally. Terminalia as in Figs. 3, 9, 10. Anterior process of aedeagus relatively small when compared to posterior process.

Allotype female.—Similar to holotype except for reproductive structures and relatively short hairs on the dorsal surface of the hindtibia. Wing length 6.6 mm.

← Figs. 7–14. Aedeagi, sinistral profiles. 7, *Sepedon f. fuscipennis*, lectotype (MCZ). 8, *Sepedon f. fuscipennis*, Victoria, Texas (USNM). 9, *Sepedon f. nobilis*, paratype, Norman Wells, Northwest Territories (CNC). 10, *Sepedon f. nobilis*, paratype, Oakland Co., Michigan (USNM). 11, *Sepedon fuscipennis* (intermediate specimen), Lafayette, Indiana (USNM). 12, *Sepedon floridensis*, Grassy Lake, Hempstead Co., Arkansas (USNM). 13, *Sepedon tenuicornis*, Oswego, New York (CU). 14, *Sepedon gracilicornis*, paratype, Mackinac Co., Michigan (CU).



Figs. 15–19. Left hindlegs. 15, *Sepedon floridensis*, Highlands Hammock State Park, Florida (CU). 16, *Sepedon f. fuscipennis*, Tampa (CU). Left antennae. 17, *Sepedon tenuicornis*, Oswego, New York (CU). 18, *Sepedon gracilicornis*, paratype, St. Mary's Pond, Oswego Co., New York (CU). 19, *Sepedon f. fuscipennis*, Laurel, Maryland (USNM).

Holotype.—♂, California, Sierra Co., 3.5 mi NW of Sierraville, Sept. 22, 1966, elev. 4900 ft., AS-538, T. W. Fisher-R. E. Orth. National Museum of Natural History, no. 101271.

Allotype.—♀, California, Sierra Co., 2 mi W of Sierraville, pasture N of hwy., Aug. 23, 1967, elev. 4940 ft., AS-628, T. W. Fisher-R. E. Orth. Deposited with holotype.

Paratypes. CANADA. BRITISH COLUMBIA: 6 mi W of Terrace, Gagnon Rd., June 23, 1960, J. G. Chillcott (2 ♀, 1 ♂), and June 24, 1960, G. E. Shewell (2 ♀, 1 ♂). MANITOBA: Whitewater Lake, 4 mi N of Whitewater, July 30, 1958, J. G. Chillcott (4 ♀, 2 ♂). NORTHWEST TERRITORIES: Norman Wells, June 25, 1969 (1 ♀), July 1, 1969 (1 ♂), July 2, 1969 (1 ♀), G. E. Shewell. SASKATCHEWAN: Waskesiu R., Aug. 1974, R. Coleman (2 ♀, 2 ♂). USA. CALIFORNIA: Sierra Co., 2 mi W of Sierraville, pasture N of hwy., elev. 4940 ft., Aug. 23, 1967, AS-628, T. W. Fisher-R. E. Orth (1 ♀, 7 ♂); Sierra Co., 3.5 mi NW of Sierraville, elev. 4900 ft., Sept. 22, 1966, AS-538, T. W. Fisher-R. E. Orth (1 ♂). IDAHO: Chatcolet, Aug. 15, 1915, A. L. Melander (4 ♀, 5 ♂). OREGON: Klamath Co., Klamath Game Refuge, elev. 4540 ft., Aug. 7, 1968, AS-743, T. W. Fisher-R. E. Orth (10 ♀, 11 ♂); Marion Co., 0.5 mi W of Mill City, Hwy. 22, elev. 900 ft., July 11, 1970, AS-858, T. W. Fisher-R. E. Orth (2 ♀, 5 ♂). MICHIGAN: Oakland Co., July 29, 1934, G. C. Steyskal (1 ♂). Deposited in Agriculture Canada, California Academy of Sciences, Cornell University, Kent State University, National Museum of Natural History, and the University of California at Riverside.

Variation.—Parafrontal spot varies from no mark to distinct black spot. Specimens from Canada and the west usually without a distinct spot. Those from eastern U.S., especially along the southern limits of distribution, have a definite black spot.

Etymology.—This species name is from the Latin *nobilis* and means well known. It refers to its widely known distribution.

Distribution.—The known range extends from Alaska and Northwest Territories, east to Newfoundland, south to New York, west to Nebraska, New Mexico, and California. This subspecies range extends further north than any other species of the *Sepedon fuscipennis* group. Its northernmost location is Aklavik, Northwest Territories (68°15' latitude).

Diagnosis.—The males of this subspecies are readily separated from *Sepedon f. fuscipennis* by aedeagal differences. Females can only be separated when collected with males by association. The distribution is nearly allopatric with *S. f. fuscipennis*. This simplifies most subspecies separations except where "intermediate specimens" are encountered. In the material examined, only once did *Sepedon f. fuscipennis* and *S. f. nobilis* occur together or overlap; that was at Jasper-Pulaski Game Preserve, Indiana, where one specimen of each was recorded. The illustrations of the terminalia of *S. f. fuscipennis* by Fisher and Orth (1983) are actually *S. f. nobilis*.

Specimens examined.—1019.

***Sepedon fuscipennis*, "intermediate specimens"**

Figs. 11, 20

A series of intermediate specimens form a narrow distribution band at approximately 40° latitude. Collection sites were from Kansas (Lawrence) east through

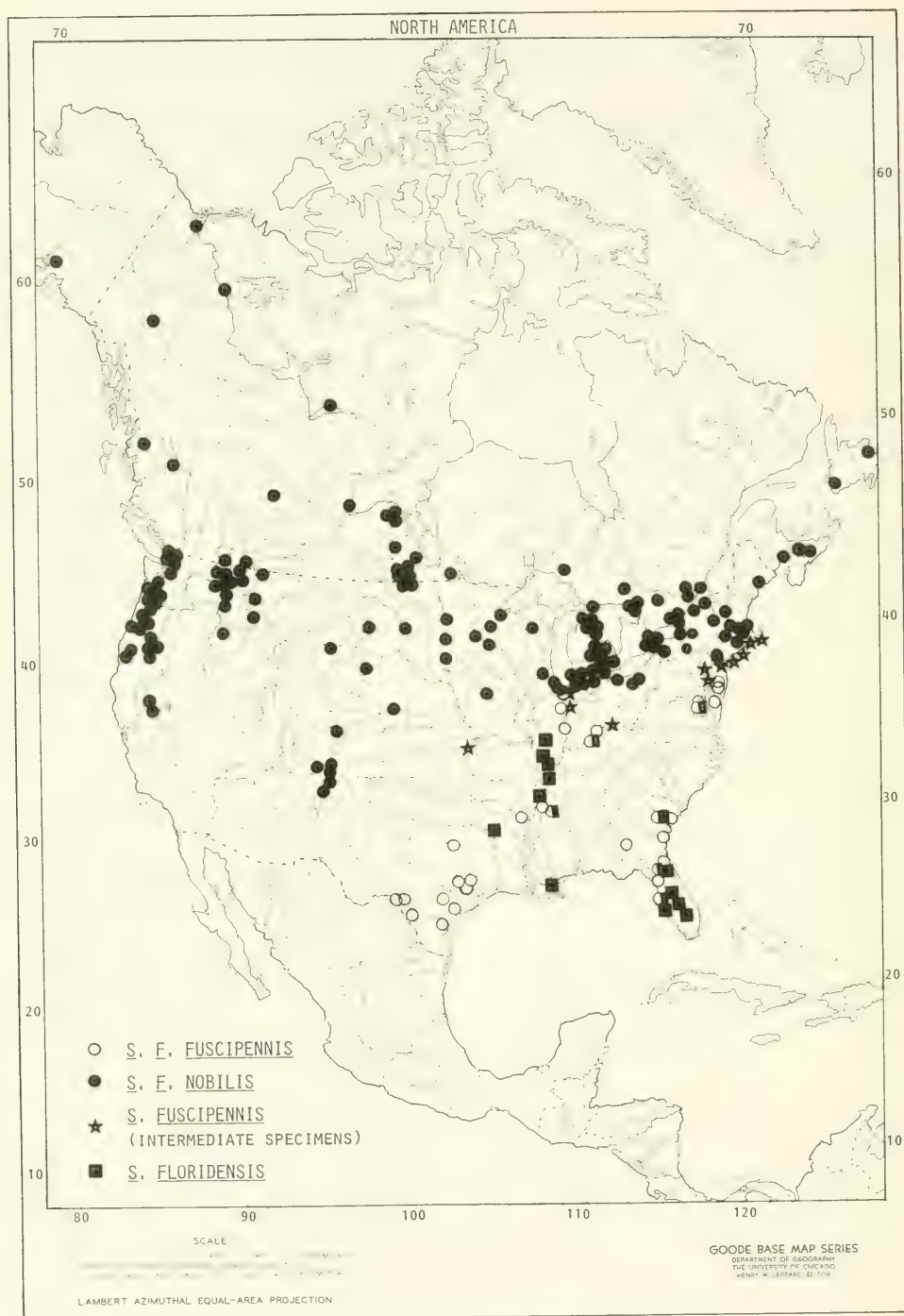


Fig. 20. Collection sites for *Sepedon f. fuscipennis*, *S. f. nobilis*, *S. fuscipennis* (intermediate specimens) and *S. floridensis*.

Illinois, Indiana, southern Ohio, Pennsylvania, New York (Long Island) to Massachusetts (Siaconset, Nantucket Is.). These specimens usually have a distinct black parafrontal spot. Males are separated by the terminalia as in Fig. 11. Females can only be separated when collected with males by association. It seems appropriate to recognize these as "intermediate specimens" rather than trying to place them to the nearest subspecies.

Specimens examined.—53.

Sepedon gracilicornis Orth, NEW SPECIES

Figs. 4, 14, 21

Holotype male.—Gross aspect tawny brown. Head with broadly excavated frons with weak ridges. Parafrontal spot represented by light brownish, elongated, velvety stain. Second antennal segment approximately 4 times as long as wide. Arista with dense, short, white hairs.

Thorax tomentose, dorsally with 2 longitudinal brown stripes. Prosternum with a few scattered setae in lower half. Pleura pale brown with sparsely scattered small setae, except metapleuron and hypopleuron are bare. Scutellum with 2 apical bristles.

Coxae yellowish white, tomentose. Legs uniformly yellowish brown. Ventral side of hindfemur with double row of heavy spines. Hairs relatively short on dorsal surface of hindtibia.

Wing length 6.3 mm. Membrane brownish, hyaline; costal margin and wing veins brownish. Area around crossveins clouded, also a cloud around apex of vein R_3 .

Abdominal segments brownish, darker dorsally. Terminalia as in Figs. 4, 14. The aedeagus, when viewed laterally, appears to have a long anterior horn or conical-like projection.

Allotype female.—Similar to holotype except for reproductive structures and parafrontal spot distinct, dark brown. Wing length 6.6 mm.

Holotype.—♂, Michigan, Livingston Co., E. S. George Reserve, May 28, 1944, George Steyskal. National Museum of Natural History, no. 101272.

Allotype.—♀, Michigan, Livingston Co., Hamburg, April 8, 1934, George Steyskal. Deposited with holotype.

Paratypes. CANADA. ONTARIO: 3 mi N Port Severn, May 18, 1959, J. G. Chillcott (3 ♀, 3 ♂); Six Mile Lake, 6 mi N Port Severn, May 1, 1959, J. G. Chillcott (1 ♂); Seeley Bay, July 27, 1952, G. C. Steyskal (1 ♀). QUEBEC: Beechgrove, May 15, 1961 (3 ♀), May 10, 1962 (1 ♂), J. R. Vockeroth; Beechgrove, May 11, 1965, collector ? (1 ♂); Beachgrove [sic], May 17, 1961, B. Poole (1 ♂). USA. CONNECTICUT: New Haven Co., Guilford, Rt. 146 nr. Moosehill Rd., June 19, 1968, K. Valley (1 ♀, 1 ♂); Old Saybrook, marsh, Sept. 5, 1968, K. Valley (1 ♀). OHIO: 1.0 mi N of Kent, May 24, 1962, B. A. Foote (1 ♂); 5 mi SE of Kent, July 4, 1965, W. Robinson (1 ♀, 1 ♂); Portage Co., Dollar Lake, Aug. 9, 1962, D. Miletich (1 ♂). IOWA: Hancock Co., Pilot Knob State Park, sphagnum bog, Sept. 23, 1969 (2 ♂), May 22, 1970 (1 ♀, 4 ♂), C. O. Berg. MICHIGAN: Alpina, July 30, 1953, G. C. Steyskal (1 ♀); Barry Co., Fish Lake, Aug. 4, 1959, R. J. Snider (1 ♂); Berrien Co., Stevensville, April 28, 1963, G. C. Eickwort (1 ♀); Livingston Co., Geo. Res., Sept. 4, 1938, G. C. Steyskal (1 ♂); Livingston Co., Hamburg, April 8, 1934, G. C. Steyskal (2 ♂); Mackinac Co., 7 mi NW of St. Ignace on Hwy. 2, June 20, 1968,

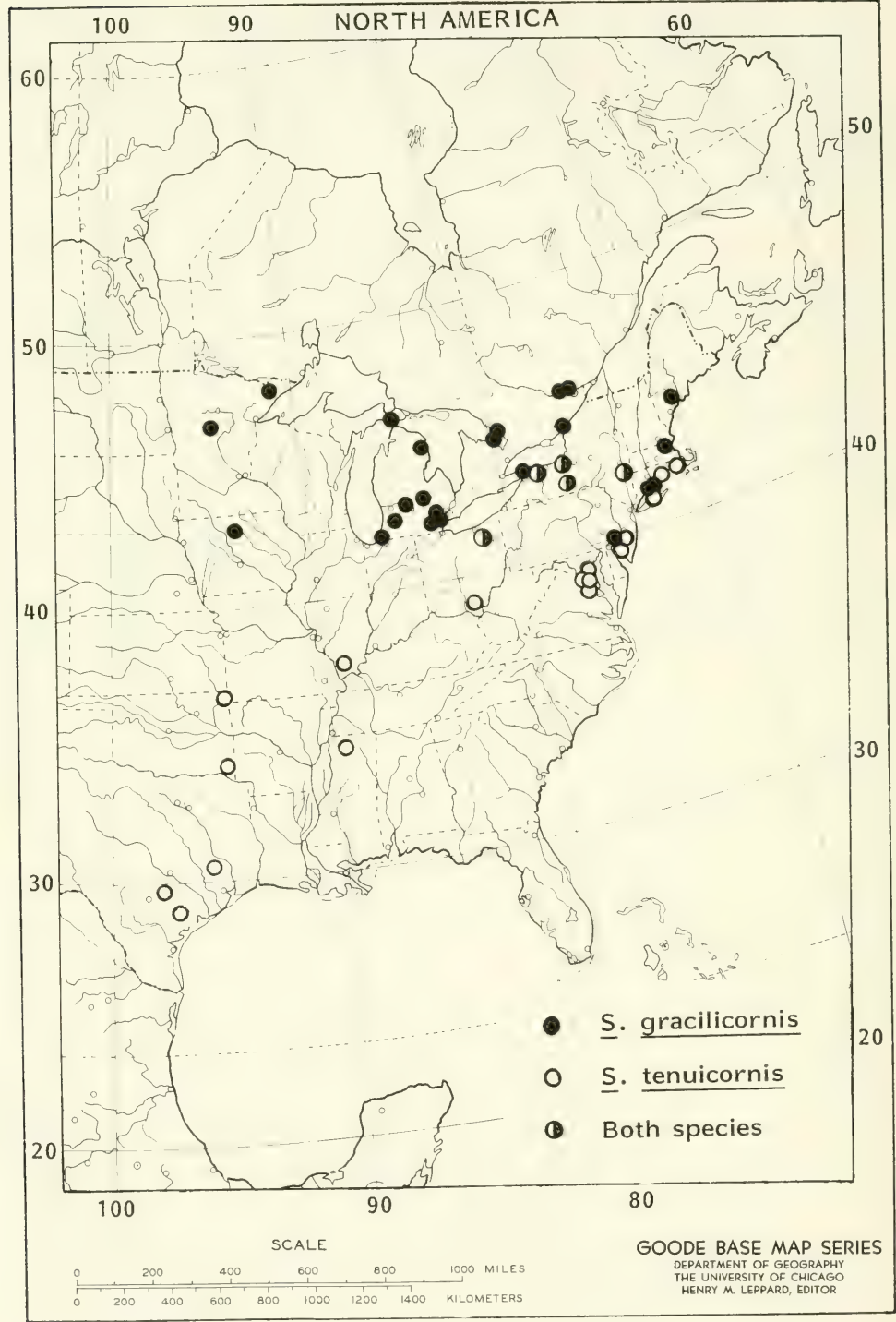


Fig. 21. Collection sites for *Sepedon gracilicornis* and *S. tenuicornis*.

C. O. Berg (3 ♀, 2 ♂); Shiawassee Co., T5N, R1E, Sec. 21, March 18, 1969, Norman T. Baker (1 ♂); Washtenaw Co., Little Portage Lake, Oct. 7, 1937, I. J. Cantrall (1 ♂). NEW YORK: Holly, July 10, 1981, L. Pechuman (1 ♂); Oswego Co., St. Mary's Pond, July 18, 1967, collector ? (1 ♂). Deposited in Agriculture Canada, Cornell University, Kent State University, National Museum of Natural History, and the University of California at Riverside.

Variation.—Parafrontal spot varies from light brown to black. Specimens from the southern limits of distribution have darker spots. Wing length 5.8–6.5 mm in males, 6.1–7.2 mm in females.

Etymology.—This species name is from the Latin *gracil*—slender + *corn*—horn; it refers to the anterior projection of the aedeagus as seen in Fig. 11.

Distribution.—The known range extends from Minnesota east to Maine including southern Ontario and Quebec, south to New Jersey, west to Iowa. The southernmost known locality of this species is Riverton, New Jersey (40.01°N latitude).

Diagnosis.—The intermediate size ratio, i.e. length to width, of the second antennal segment separates it from other members of the *S. fuscipennis* group. Frequently, when the terminalia have been cleared in preparation for viewing, the ultimate segment distends itself as in Fig. 4. *Sepedon gracilicornis* is a more boreal species than *S. tenuicornis*, from which it is here separated. The illustration of the terminalia of *S. tenuicornis* by Steyskal (1951) [1950] is actually *S. gracilicornis*.

Specimens examined.—65.

***Sepedon tenuicornis* Cresson**

Figs. 5, 13, 21

Sepedon tenuicornis is found east of 100° longitude. The known northern limit of its distribution is New York near the southern shores of Lake Ontario. It is found as far south as southeastern Texas. It has not been recorded from extreme southeastern United States or Canada.

The holotype male terminalia were examined and agree well with Figs. 5, 13. Wing length 6.4 mm. Collection data for the holotype: Little Falls, District of Columbia, August 22, 1915, W. L. McAtee, National Museum of Natural History, Type no. 29507. I have also viewed 5 of the paratypes selected by Cresson from or near Plummer's Island, Maryland, and all compare well with the holotype.

Diagnosis.—The slender second antennal segment of *S. tenuicornis* separates it from all other members of the *S. fuscipennis* group. The segment is approximately 5 times longer than wide.

Specimens examined.—96.

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Florida; H. J. Teskey, Biosystematic Research Institute, Agriculture Canada, Ottawa, Ontario. I express my gratitude to C. O. Berg and L. Knutson for kindly reviewing the manuscript and for their many helpful comments. A special thanks to T. W. Fisher, University of California Riverside, for his support and counsel.

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**OCCURRENCE OF ADULT AMERICAN DOG TICK,
DERMACENTOR VARIABILIS (SAY), AROUND SMALL
MAMMAL TRAPS AND VERTEBRATE CARCASSES¹**

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Abstract. — We report on the distribution of unfed adult American dog ticks, *D. variabilis*, in a wet meadow in which meadow voles, *Microtus pennsylvanicus*, were being live-trapped. Areas of 0.3 m radius around Fitch and Sherman® small mammal live traps were each visually searched for ticks for 30 s, as were an equal number of similar circles halfway between traps. In 1981 and 1982, 482 ticks were found around traps and 3 in intertrap circles. In 1983, 20 ticks were around traps and 1 between traps. During July, 1981, 48 of 50 traps had ticks around them, while no ticks were found in the intertrap circles. Unfed *D. variabilis* adults were also observed around vertebrate carcasses, including those of various fish and a black rat snake, *Elaphe obsoleta obsoleta*. *D. variabilis* adults moved into cages baited with dead fish and assumed questing attitudes; no ticks were found in the unbaited cages. In mid-May 1984 unfed *D. variabilis* adults were found within 1 m of the carcass of a white-tailed deer, *Odocoileus virginianus borealis*, which had died during the winter when *D. variabilis* adults are not on hosts.

Smith et al. (1946) reported that American dog tick, *Dermacentor variabilis* (Say), adults were apparently attracted to animal odors, such as urine. Although Sonenshine et al. (1966) in Virginia found *D. variabilis* adults to be relatively sedentary, they suggested that these ticks might traverse short distances to sources of attraction. Our observations of numbers of *D. variabilis* adults around small mammal live traps and vertebrate carcasses prompted us to investigate the distribution of *D. variabilis* adults around live traps in a meadow and their possible attraction to vertebrate carcasses. The ability to influence tick distribution under field conditions might have applications in managing their populations.

MATERIALS AND METHODS

The study area.—The study site at the Patuxent Wildlife Research Center in Laurel, Maryland, fit Hotchkiss and Stewart's description (1979) of a sweetgum field, the successional stage between a wet meadow and an immature seepage

¹ This paper reflects the results of research only. Mention of a proprietary product or a pesticide does not constitute an endorsement or a recommendation of this product by the USDA.

swamp. The field contained a variety of wet meadow plants, including an abundance of grasses, and scattered sweetgum, *Liquidambar styraciflua* L., saplings and autumn olive, *Elaeagnus umbellata* Thunb., bushes. The field was bordered on two sides by a mature deciduous hedgerow. Most of the borders of the other two sides were two man-made ponds, one of which had a ca. 2 m high dike. Adjacent to the dike was a narrow (1.5–2 m) wetter strip of the meadow, where sedges and rushes grew. The surrounding woodlands were bottomland forest and beech-white oak forest.

Distribution of ticks around live animal traps.—A 0.8 hectare grid containing 100 Fitch traps was established in the meadow 1 year prior to the start of this tick study for a capture and release population study of meadow voles, *Microtus pennsylvanicus* (Ord) (Nichols et al., 1984). Voles were trapped and released in the grid for three or five consecutive days monthly through 1983. The traps were in 10 rows of 10 traps each, and each trap was 7.6 m from the adjacent traps in its row and column. Each trap contained a handful of hay and dried grass, and was left open between monthly trapping periods, thus allowing voles free access. During the second year of the study the Fitch traps, which were being tipped over by deer, were replaced with Sherman traps, and four raccoon traps were placed on the grid.

To assess the distribution of *D. variabilis* adults within the trapping grid, we visually searched for ticks within a 0.3 m radius from the approximate center of a trap. Nine to 50 trap areas were searched on any given day. Each area was searched for 30 s. If no ticks were detected after 25 s, the searcher lightly brushed his hand and arm through the vegetation in the search area to pick up unseen questing ticks which were immediately released in the circle. On the same day this search procedure was repeated for an equal number of circles of the same area halfway (3.8 m) between traps in the same rows or columns. A total of 12 counts were made June–August in 1981, June and July of 1982, and in July 1983.

Movement of ticks to animal traps.—*D. variabilis* adults were collected by flagging at the study site, and each marked with an enamel dot of any of three colors. At each of the cardinal directions a group of seven ticks was released 0.3, 0.6 and 1.2 m from the approximate center of a Fitch trap. The colors of the dots denoted the distance the ticks were released from the trap. A circular area with the trap as center was searched for marked ticks 1, 5 and 7 d after their release. The innermost area (<0.3 m from the trap) was searched for about 1 min, the middle area (a ring, 0.3–0.6 m from the trap) for 3 min, the outer area (a ring, 0.6–1.2 m from the trap) for 11 min and 5 min were spent searching beyond 1.3 m from the trap. This procedure was repeated at a second trap, except the recaptures were attempted only on the day following release.

Attraction to animal carcasses.—To determine if *D. variabilis* adults were attracted to non-mammalian vertebrate carcasses, two dead fish were placed inside a cage (25 cm long, 10 cm diam) of hardware cloth (0.64 cm mesh) in the meadow. A larger cage (1.3 m high, 1.1 m diam) of hardware cloth was centered over the smaller cage. The outer cage was open on the bottom and the inner and outer cages were held in place by wires pushed into the soil. An identical pair of unbaited cages was placed 1 m from the one described. We wore vinyl gloves and plastic wrist-to-elbow sleeves when constructing and setting out the cages in order to

Table 1. *D. variabilis* adults observed around (0.3 m radius) small mammal traps and within circles of the same radius between traps.^a

Date	No. Traps and Intertrap Circles	No. Ticks ^b <0.3 m from Traps	Avg. No. Ticks/Trap	% Traps with Ticks	No. Ticks in Intertrap Circles	Avg. No. Ticks/Circle	% Circles with Ticks
(1981 and 1982)							
June 7	15	11	0.7	53.3	1	0.07	6.7
June 21	9	91	10.1	100	0	0	0
June 22	30	44	1.5	50	1	0.03	3.3
June 23	20	27	1.4	55	0	0	0
July 7	30	156	5.2	96.7	0	0	0
July 16	20	114	5.7	95	0	0	0
Aug. 13	50	17	0.3	28	1	0.02	2
Aug. 18	15	36	2.4	73.3	0	0	0
(1983) ^c							
July 5	20	8	0.4	20	0	0	0
July 11	30	8	0.3	20	0	0	0
July 12	20	3	0.2	15	1	0.05	5
July 13	14	1	0.1	7.1	0	0	0

^a Traps were 7.6 m apart and circles were midway between traps.

^b A total 230 ♂, 256 ♀ were found around traps and 2 ♂, 1 ♀ in intertrap circles in 1981 and 1982, and in 1983 10 ♂, 10 ♀ around traps and 1 ♂ in circles.

^c Data from 1983 presented separately, because by that time vole and tick populations had declined dramatically (Nichols et al., 1984).

avoid contaminating the cages with our perspiration or skin oils. Two fish were added to the baited cage 6 and 12 d after the initial baiting. Black crappie, butterfish and ocean perch were used as bait. The cages and the vegetation within and 0.3 m outside the cages were searched for ticks before and periodically after the initial baiting. The *D. variabilis* population at the study site collapsed in 1983, so this procedure was not repeated until 1984.

A large concentration of ticks was found around the carcass of a white-tailed deer, *Odocoileus virginianus borealis* Miller, in mid-May. *D. variabilis* adults within 1 m of the carcass were counted periodically through August.

RESULTS

Distribution of ticks around live animal traps.—*D. variabilis* adults were repeatedly present in considerable numbers around the small mammal traps, but found infrequently in the areas between traps (Table 1). The numbers of ticks around the traps changed seasonally, in accordance with reported cycles (Sonenshine et al., 1966), but few ticks were ever observed in the intertrap circles. In early and mid-July 1981, ticks were seen around 48 of 50 traps that were checked; averaging 5.4 ± 4.8 ticks per trap. During the same period no ticks were found in an equal number of stations between traps. As many as 34 ticks (16 ♂, 18 ♀) were seen within 0.3 m of a trap and as many as 11 ticks on a blade of grass. Most ticks seen around traps were 4–6 cm above the ground. They were rarely on the traps, but were frequently on vegetation hanging over the traps. It was not feasible to monitor the frequency and duration of visitations by voles to individual

traps. Voles were abundant in 1981 and 1982, and the population crashed by 1983 (Nichols et al., 1984). The raw data of Nichols et al. (1984) show trap catches of >70% on given dates during peak vole abundance.

Movement of ticks to animal traps.—Although some ticks moved more than 1 m in a day, there was no strong pattern of movement of marked *D. variabilis* adults toward the Fitch traps. One day after release less than half of the marked ticks were found within 1.2 m of traps (i.e. the furthest points of release). Only 11 and 13 marked ticks were found within 0.3 m of the Fitch traps. One trap was checked only the day after the ticks were released, but a week after release 13 of 15 marked ticks found less than 1.2 m from the second trap were within 0.3 m of it.

Attraction to animal carcasses.—Table 2 shows the attraction of *D. variabilis* adults to the fish carcasses in the hardware cloth cage in the meadow. In the first trial, 3 d after the fish were placed in the cages, just one tick was found on the outer cage of the baited set and none in either of them. No ticks were ever found in, on or within 0.3 m of the unbaited cage. Ten days after the initial baiting, six *D. variabilis* adults were observed inside the baited cage and clustered on vegetation above the fish. One week later eight ticks (5 ♂, 3 ♀) were in the cage with the fish. Except that on two occasions one tick was found within 0.3 m of the cage, similar results were obtained in the second trial.

D. variabilis adults were also found clustered around a dead black rat snake, *Elaphe obsoleta obsoleta* Say, and none 1–2 m away; further evidence of attraction to non-mammalian carcasses.

On May 19, 1981, 194 unfed *D. variabilis* adults were found within 1 m of the carcass of a white-tailed deer. The carcass was first noticed when fresh the previous January, a period when adult *D. variabilis* are not on hosts. The number of ticks around the carcass gradually decreased in ensuing weeks. On May 28 there were 155 ticks within 1 m of the carcass, while on June 21, 87 ticks, on June 30, 39 ticks and September 2, 20 ticks within 1 m of the carcass. The following spring there were still 10 ticks within 1 m of the carcass. Between May 19 and June 3 two ticks found, marked and released 6 m away from the carcass as part of another study moved to within 1 m of the carcass.

DISCUSSION

A combination of factors may account for the clustering of ticks around the mammal traps: 1. Engorged nymphs drop off voles in and around traps, and remain under or near the traps until they molt into adults. We found engorged nymphs under traps on several occasions. 2. *D. variabilis* adults may be attracted, although based on our data not avidly, by odors associated with voles or by skin secretions from humans handling the traps, just as *D. variabilis* adults were attracted to stakes rubbed against dogs or soaked in their urine (Smith et al., 1946). 3. Aggregation pheromones may attract and retain ticks (Leahy et al., 1983). It is probably advantageous for adult *D. variabilis* to quest in areas of intense vole activity because of the opportunities of acquiring as hosts mammalian predators of voles.

The presence of ticks in the cages baited with fish seems to be due to attraction from outside or retention of transient ticks for five reasons: 1. We checked the vegetation under the traps for ticks when the cages were set up. 2. There was a

Table 2. Attraction of *D. variabilis* adults to fish carcasses in a 1.3 m diam cage of hardware cloth.^a

Date	No. of Ticks					
	At Cage with Fish			At Empty Cage		
	<0.3 m Outside Cage	On Cage	In Cage ^b	<0.3 m Outside Cage	On Cage	In Cage
1982 Trial						
Aug. 13 (start)	0	0	0	0	0	0
16	0	1 ♂	0	0	0	0
23 ^c	1 ♀	0	4 ♂, 2 ♀	0	0	0
30	0	0	5 ♂, 3 ♀	0	0	0
Sept. 2	1 ♀	0	2 ♂	0	0	0
14	0	1 ♀	1 ♂, 1 ♀	0	0	0
1984 Trial						
July 20 (start)	0	0	0	0	0	0
24	0	0	1 ♂	1 ♀	0	0
26	1 ♂	0	1 ♂, 4 ♀	1 ♀	0	0
Aug. 1	2 ♀	1 ♀	2 ♂, 1 ♀	0	0	0
7	1 ♂, 1 ♀	0	0	0	0	0

^a Cages were 1 m apart in meadow. We wore disposable vinyl gloves and plastic sleeves when handling the cages to prevent contamination of them with perspiration and skin secretions.

^b Ticks in the cage were concentrated within ca. 15 cm of the fish.

^c Added two fish Aug. 19 and 25.

gradual increase in numbers of ticks in the baited cages. 3. The trials were at a time when it was unlikely that engorged nymphs, if any were hidden in litter below the traps, would molt to adults and start questing. 4. It is unlikely that unfed adult ticks of both sexes dropped from hosts attracted to dead fish. 5. Most of the ticks found were well inside the outer cage (only 2 on the outer cage and 2 < 0.3 m from it) which prevented mammalian scavengers close access to the fish. In New Jersey, P. P. Shubeck (pers. comm.) noticed ticks around carrion beetle (Coleoptera: Silphidae) traps (Shubeck, 1976) baited with chicken legs or fish. Although Semtner and Hair (1975) reported that *D. variabilis* adults are attracted to CO₂, the attractive factor in decomposing vertebrates needs to be identified.

The occurrence of the large numbers of adult *D. variabilis* around the deer carcass seems due to attraction. The deer died in the winter when *D. variabilis* are not on hosts. We found no partly fed female ticks. *D. variabilis* nymphs feed on small and medium-sized mammals. The ticks around the deer carcass, therefore, probably did not drop off the deer, but subsequently arrived at the carcass. If voles visited the carcass, fed nymphs might have dropped off near it and molted into adults, however, there is no evidence for this scenario. Since scavenging mammals visit carcasses, it would be of adaptive value to the ticks to quest around a vertebrate carcass mammalian.

These data indicate that the distribution of *D. variabilis* adults at the study site was influenced by the presence of mammalian and non-mammalian vertebrate carcasses, and by the vole trapping techniques. Also, *D. variabilis* adults were attracted into cages baited with fish or transient ticks remained in them. Waladde and Rice (1982) distinguished between ticks which actively hunt for hosts and

those which wait in ambush, but the case of *D. variabilis* is still not clearly defined. A person, by avoiding the live traps, was able to walk about the trapping grid, which at times harbored many ticks, and acquire few if any *D. variabilis* adults. Further study of factors which attract *D. variabilis* adults might lead to the development of methods of regulating the local distribution of questing ticks.

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NEOTROPICAL TINEIDAE, I: THE TYPES OF H. B. MÖSCHLER
(LEPIDOPTERA: TINEOIDEA)

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Abstract.—The types of four little-known moth species described by H. B. Möschler in the family Tineidae are critically examined and illustrated. Three (*pallidus*, *ochraceus*, and *walsinghami*) are members of the large American genus *Acrolophus*; the fourth (*Pexicnemidia mirella*) has been transferred to the former yponomeutoid genus *Urodus*. *Acrolophus walsinghami* is synonymized under *A. triatomellus* (Walsingham) (new synonymy).

This contribution initiates a series of reports designed to investigate and reveal a major faunal component of the Neotropical Region. The series will consist of faunal studies, generic revisions, biological observations, and reports (such as the present one) on poorly known tineid taxa described by previous workers. Ultimately the series will comprise a major treatise on the neotropical Tineidae.

Currently, 84 genera and 455 species of Tineidae are recognized (Davis, 1984) from the Neotropical Region, including all of South America and Mexico as well as marginal records from the extreme southern United States. Since 1963, the author has led eight separate collecting trips to the neotropics, with several more planned. In recent years I have also supported through Smithsonian Institution grants several colleagues who have assisted me in a much needed survey of the Neotropical Region. Results from these initial efforts suggest at least 75% of the West Indian and Central American and from 85 to 90% of the South American tineid faunas are unnamed. These minimal estimates indicate a total fauna for the Neotropical Region of about 2400 species, most of which are yet to be collected.

Although several species of Tineidae are serious economic pests of both animal and plant products, the vast majority of neotropical species are ground level detritus feeders. They, along with innumerable other soil organisms, thus serve a vital function in the recycling of organic matter and in the basic production of soils in the fragile tropical ecosystem.

Institutional acronyms referred to in this paper are: BMNH for British Museum (Natural History), London, England; MGAB, Muzeul de Istorie naturala "Grigore Antipa," Bucharest, Romania; NHMV, Naturhistorischen Museum, Vienna, Austria; USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C., USA; ZMHB, Zoologischer Museum, Humboldt Universität, Berlin, Germany (DDR).

NEOTROPICAL TINEIDAE TREATED BY H. B. MÖSCHLER

The German lepidopterist H. B. Möschler wrote three major faunal works on neotropical Lepidoptera. Two of these, treating Surinam (1876-1882) and Puerto

Rico (1890), contained descriptions of Tineidae. Of the seven new species originally included in the Anaphoridae, Tineidae or "Tinaceae" by Möschler, only four remained in the family until recently. Three of these are members of the large neotropical genus *Acrolophus*, and one, *Pexicnemidia mirella* Möschler, was found by the author to be a species of *Urodus* and was so treated in the recent Neotropical Checklist (Heppner, 1984). Möschler also mentioned several other "tineoid" names, most of which have been correctly assigned to other families. However, three names (*Acrolophus plumifrontella* (Clemens), *Anaphora popeanella* (Clemens) and *Myrmecozela ochraceella* Tengstrom) have persisted in the Latin American literature down to the present. Because none of the three are believed to occur in Latin America but are probably misidentifications, they were omitted from the recent Neotropical Checklist. All were determined by Möschler from specimens collected in Puerto Rico. Although Möschler's tineid types are preserved in the collections of Humboldt University (ZMHB) and were examined in the course of this study, specimens from Puerto Rico identified by Möschler under the preceding three names could not be located. Both *Acrolophus plumifrontella* and *A. popeanella* are common North American insects for which I know of no authentic examples from the West Indies. The only North American *Acrolophus* which I have verified from the Antilles is *A. arcanella* (Clemens). Several specimens of this species from Cuba exist in the USNM and Forbes (1931) mentions its occurrence in Puerto Rico. Möschler's "*A. plumifrontella*" could refer to the very similar and closely related *A. mimasalis* (Walker) described from the Dominican Republic and tentatively reported from Puerto Rico by Forbes (1930). His *A. popeanellus* may have represented an undescribed species. The European *Myrmecozela ochraceella* Tengstrom likewise presents a problem in lieu of actual Puerto Rican specimens. Possibly it represented a pale example of *Xystrologa antipathetica* (Forbes), a common myrmecozeline from Puerto Rico.

One other matter which needs to be mentioned concerns the family name for the large American genus *Acrolophus*. In his Puerto Rican paper, Möschler (1890) included *Acrolophus* and its allies in the family Anaphoridae, thus raising the status of the group name first proposed by Walsingham (1887) as a subfamily within Tineidae. Probably because Meyrick synonymized *Anaphora* (along with 15 other names) under *Acrolophus*, Walsingham (1914), not wishing to base a familial name on a junior synonym, later renamed the family Acrolophidae. Although Anaphorinae (and Anaphoridae) clearly has priority and is available, the familial name Acrolophidae, or Acrolophinae, has been used consistently to the present day—a usage that I hope will be conserved.

Acrolophus pallidus Möschler

Figs. 1, 7–10

Acrolophus pallidus Möschler, 1881: 438.—Walsingham, 1887: 153; 1914: 383.—Dalla Torre and Strand, 1929: 25.—Davis, 1984: 20.

The unique female holotype, missing the abdomen and deposited in ZMHB, has been examined and compared to conspecific specimens in the USNM. *Acrolophus pallidus* is most closely allied to *A. vigia* Beutelspacher, reared from orchid roots in Mexico, and an undescribed species from Colombia in the USNM also reared from orchid roots. All three species are similar in possessing light



Figs. 1-6. Adults. 1, *Acrolophus pallidus*, holotype ♂, Surinam, length of forewing 14.5 mm. 2, *A. ochraceus*, holotype ♂, Puerto Rico, length of forewing 11.5 mm. 3, *A. triatomellus*, lectotype ♂ of *A. walsinghami*, Puerto Rico, length of forewing 7 mm. 4, *A. triatomellus*, syntype ♂, St. Thomas, length of forewing 4.2 mm. 5, *A. triatomellus*, syntype ♀, St. Thomas, length of forewing 10 mm. 6, *Urodus mirella*, lectotype ♂, Puerto Rico, length of forewing 7.2 mm.

brown, more or less speckled forewings and dark fuscous hindwings in both sexes. The female labial palpi of *A. pallidus* are very short, with those of the male more than twice as long and terminating at the vertex well short of the occiput.

Walsingham (1914) reported *A. pallidus* from Costa Rica; upon examination, this specimen (USNM) proved to be *A. vigia* and represents a southward extension of the latter's range. Consequently, the distribution of *A. pallidus* is still restricted to the Guiana coastal plain. The male genitalia figured is from a specimen collected at St. Jean, French Guiana which was also mentioned by Walsingham (1914). The female of this species is unknown.

Additional material examined: French Guiana: St. Jean, Maroni: 1 ♂, Schaus Collection (USNM). St. Laurent du Maroni: 2 ♂, Dognin Collection (USNM).

***Acrolophus ochraceus* (Möschler)**

Figs. 2, 15–19, 22

? *Caenogenes ochracea* Möschler, 1890:337. — Walsingham, 1891: 514; 1897: 170. *Acrolophus ochracea* (Möschler). — Wolcott, 1923: 207; 1936: 504. — Davis 1894: 20.

Acrolophus (*Caenogenes*) *ochraceus* (Möschler). — Forbes, 1930: 162. — Wolcott, 1951: 743.

Acrolophus ochraceus was described from a single male, labelled simply 'Portorico,' and now deposited in the collections of ZMHB. Möschler originally placed *A. ochraceus* in Walsingham's genus *Caenogenes*, which was later synonymized by Meyrick (1912: 191) along with 15 other names under *Acrolophus*. Forbes (1930) maintained *Caenogenes* as a subgenus of *Acrolophus*.

Even in a genus as large and diverse as *Acrolophus*, this species stands out. Its generally pale yellowish brown color and relatively straight forewing termen contrasts sharply with most other acrolophine species. The labial palpi of the male are extremely elongate, extending over the head between the antennae to the posterior margin of the mesonotum. The female differs in having labial palpi only slightly upturned and of normal length (less than one third the length of the male). The dorsal vestiture of the female hindwings is also much darker (light fuscous) instead of tawny. The male genitalia are unusual in demonstrating considerable asymmetry in a genus largely devoid of such variation. The female genitalia was illustrated from the specimen listed below from Rio Piedras.

Additional material examined: PUERTO RICO: 7 km. S. Ciales, 3200' [976 m]: 1 ♂, 22 July.–22 Aug. (USNM). Laguna Guajataca, Boy Scout Camp, 205 m: 1 ♂, 2–5 Apr. (USNM). Maricao State Forest: 1 ♂, 22 June (USNM). Palmas Abajas (near Guayama), 1900' [579 m]: 1 ♂, 16 Aug. (USNM). Reserva Forestal Guajataca, 360 m: 1 ♂, 18–28 Mar. (USNM). Rio Piedras, Insect Experiment Station: 1 ♀, 13 Apr. (USNM). San Juan: 1 ♂, 15 Sept. (USNM).

Forbes (1930) and Wolcott (1936) list additional collecting localities.

***Acrolophus triatomellus* (Walsingham)**

Figs. 3–5, 11–14, 23

Anaphora triatomella Walsingham, 1897: 172. — Strand, 1929: 22.

Acrolophus triatomellus (Walsingham). — Forbes, 1930: 163; 1931. — Wolcott, 1936: 504; 1951: 743.

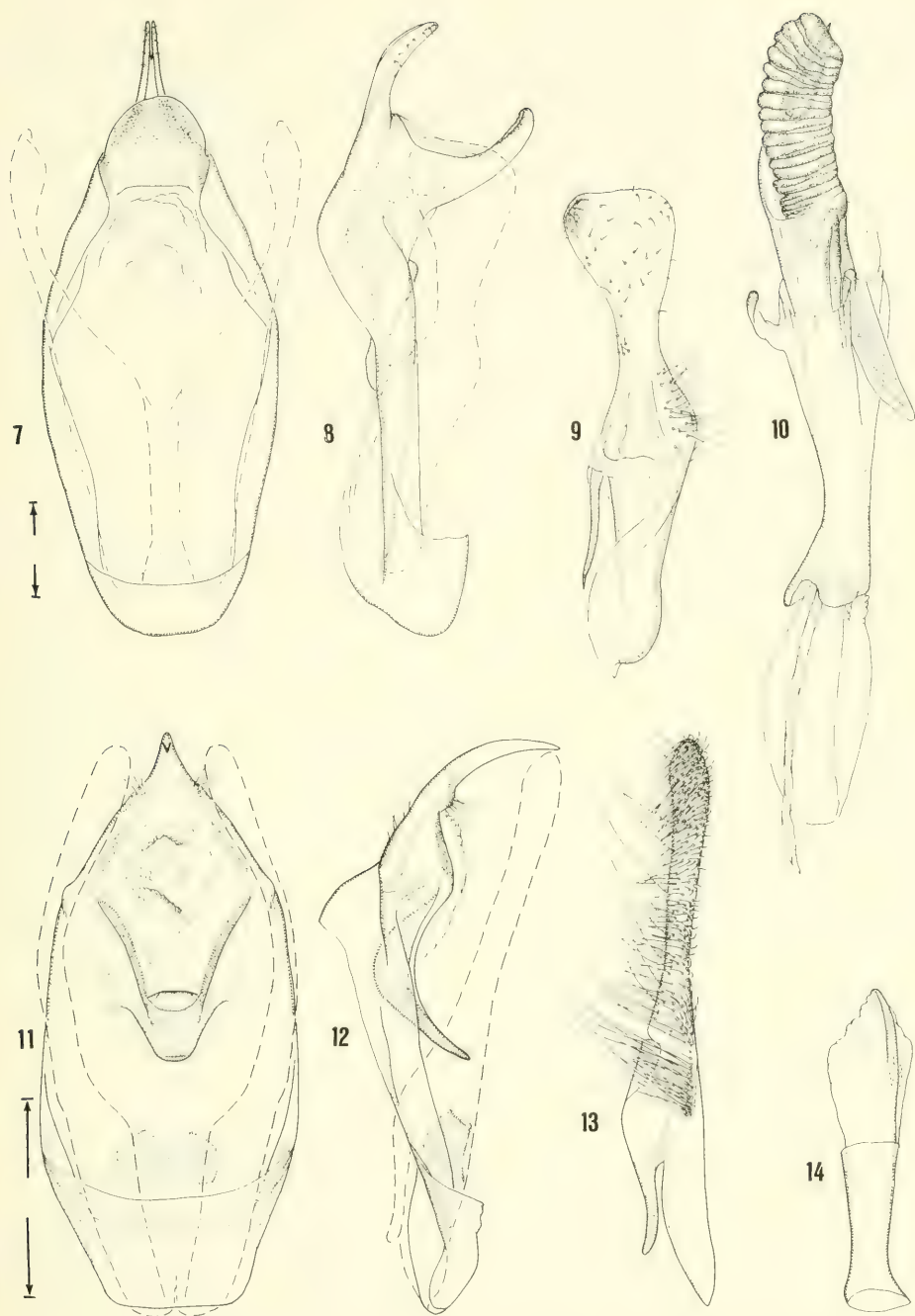
Acrolophus triatomella (Walsingham). — Davis, 1984: 20.

Acrolophus walsinghami Möschler, 1890: 336 (New synonymy). — Walsingham, 1891:514; 1897:174. — Wolcott, 1923: 207. — Strand, 1929: 26. — Forbes, 1930: 165. — Wolcott, 1936: 504; 1951: 744. — Davis, 1984: 20.

Acrolophus triformellus Forbes, 1930: 163; 1931: 391. — Wolcott, 1936: 504; 1951: 743. — Davis, 1984: 20 (synonym of *walsinghami*).

Acrolophus triformalis [sic] Forbes, 1930: 160 (misspelling of *triformellus*). — Davis, 1984: 20.

Acrolophus walsinghami Möschler was described from three male syntypes from



Figs. 7-14. Male genitalia. 7, *Acrolophus pallidus*, ventral view. 8, Lateral view. 9, Lateral view of valva. 10, Aedeagus. 11, *A. triatomellus*, ventral view. 12, Lateral view. 13, Lateral view of valva. 14, Aedeagus. All scales = 0.5 mm.

Puerto Rico. One of these, bearing a locality label 'Portorico,' a genitalia slide label no. 3454, as well as a lectotype label (by D. Davis), has been selected as lectotype. The synonymy of this name and that of *A. triatomellus* Forbes has already been noted in the Neotropical Checklist (Davis, 1984).

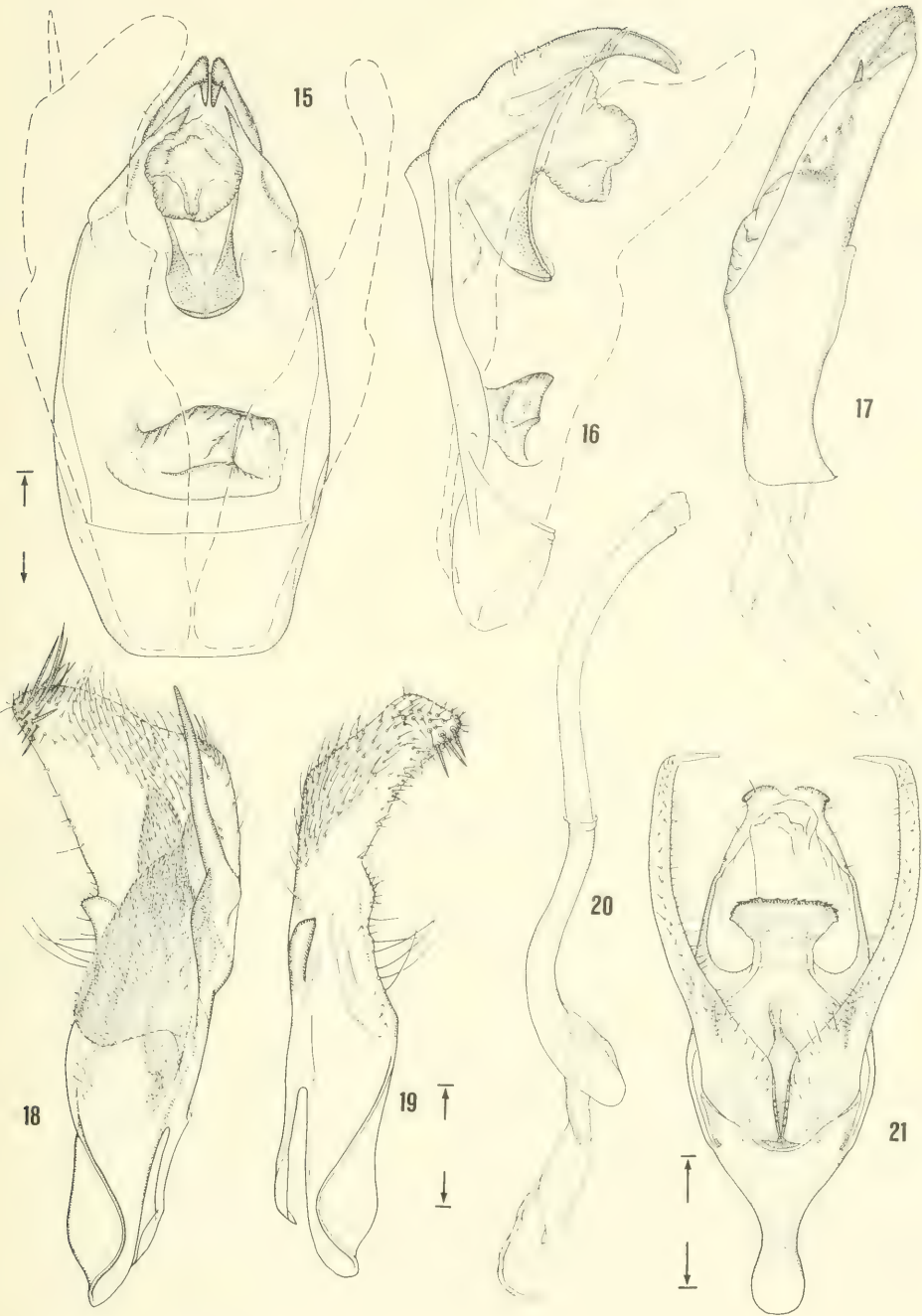
Comparison of the male lectotype of *Acrolophus walsinghami* with the type series of *A. triatomellus* indicates these two species also to be synonymous. Walsingham described *A. triatomellus* from five specimens collected on St. Thomas. As was customarily done by Walsingham, no actual holotype was selected; instead, a "type" ♂ and ♀ (now deposited in MGAB) were selected along with three "paratypes." The male "type" bearing the labels: "S. Thomas, 5.IV.94; *Anaphora triatomella* Wlsm., ♂ 1912, 109, Type; Holotype, *Anaphora triatomella* Wlsm., ♂, Romania; Lectotype ♂, *Anaphora triatomella* Wlsm., by Davis, is hereby designated as the lectotype. The remaining four specimens: 1 ♀ "allotype," 29.III.94, (MGAB); 1 ♂, 20.III.1894, (BMNH); 1 ♂, 10/4 94, (NMVM); 1 ♀, 23/3 94 (NMVM), are to be considered paralectotypes.

Acrolophus triatomellus appears to be one of the most common members of the genus occurring in Puerto Rico and the Virgin Islands. Its distribution is not known to extend beyond these islands. In the collections of the USNM are more than 100 specimens from Puerto Rico and nearly 50 specimens from Guana Island in the British Virgin Islands. The forewings of the male are quite variable from light brown with a well defined pattern to an overall dark fuscous color with almost no pattern discernible except for a pair of pale, whitish markings near the basal third of the cubital cell. The female is generally paler in color, often with indistinct forewing markings. The labial palpi of the male are recurved over the head and extend to the first abdominal segment. Those of the female are less than one third the length of the male palpi and are porrect with a slight dorsal arch.

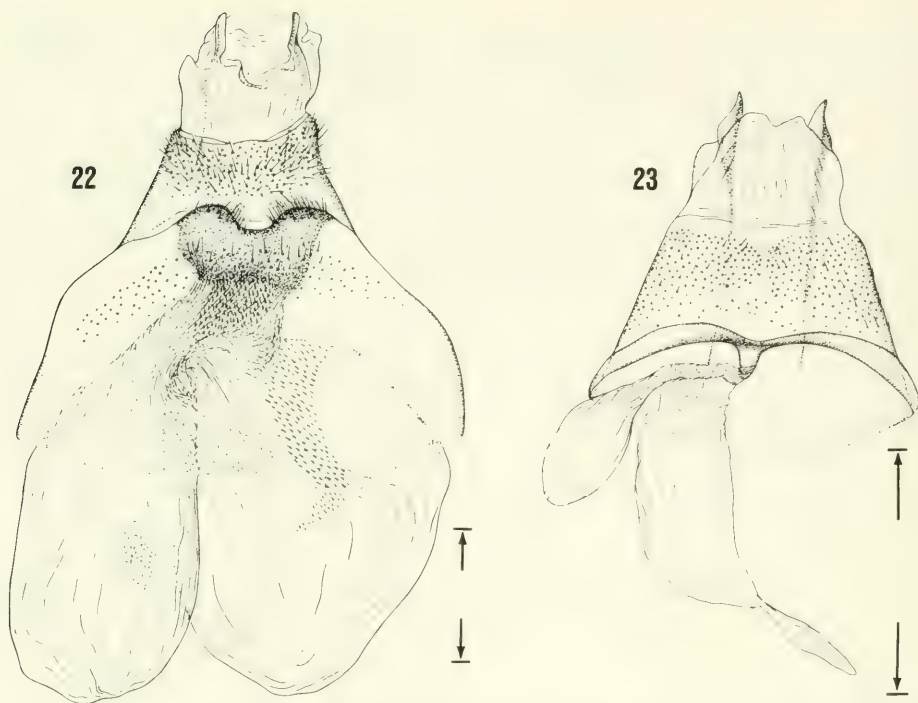
This species can be easily confused with the closely related *A. parvus* Walsingham. The male genitalia of the latter possess broader, less attenuated valvae. *Acrolophus parvus* is known to range from Dominica (its type locality) into the Virgin Islands where it overlaps with *A. triatomellus*. The former is not known to occur in Puerto Rico, although it may range as far west as St. Thomas (Forbes, 1930).

The illustrations of the male genitalia are that of the lectotype of *A. walsinghami*. The female genitalia is figured from a paratype of *A. triatomellus*.

Additional material examined: PUERTO RICO: Balneario de Jobos: 2 ♂, 16 Mar.—8 Apr. Bayamon: 9 ♂, 3 ♀, 15 Jan.—28 July. Coamo Springs: 2 ♂, 10 Apr. Guajataca Forest, Isabela: 1 ♂, 1 ♀, 22 July. Guánica Insular Forest: 1 ♂, 6 July. Isabela, Hotel Palmeriana, 60 m: 2 ♂, 1 ♀, 10–14 Mar. Isla Maguey, Parguera: 1 ♂, 18 Dec. Juquillo, 3 m: 1 ♂ 18–19 Jan. Lago Tortuguero: 1 ♂, 2 Aug. Laguna Guajataca, Boy Scout Camp, 205 m: 3 ♂, 2–5 Apr. Lajas: 1 ♂, 6 July. La Parguera, 3 m: 33 ♂, 1 ♀, 5–11 Feb. Las Marias: 1 ♂, 22 July. Luquillo Experimental Forest, Verde Field Station, 435 m: 1 ♀, 1–21 Jan. Mayaguez: 4 ♂, Jan; 4 ♂, 2 ♀, 1 July–31 Aug. Monte del Estado, near Maricao, Centro Vacacional, 650 m: 1 ♀, 1–9 Mar. Punta Jacinto, SW coast near Guánica, 3 m: 3 ♂, 27–28 Jan. 12.2 km S. Rincon, Route 115, 3 m: 2 ♂, 1 ♀, 22–28 Feb. Salinas: 1 ♂, 1 ♀, 5 Aug. San Germán: 1 ♂, 16 Apr. San Juan: 1 ♀, 15 Sept. Vieques Island, Puerto Real: 1 ♂, 29 Apr. VIRGIN ISLANDS: Guana Island: 43 ♂, 4 ♀, 1–14 July. All specimens deposited in the USNM.



Figs. 15-21. Male genitalia. 15, *Acrolophus ochraceus*, ventral view. 16, Lateral view. 17, Ae-
doeagus. 18, Lateral view of left valva. 19, Lateral view of right valva. 20, *Urodus mirella*, aedoeagus.
21, Ventral view. All scales = 0.5 mm.



Figs. 22, 23. Female genitalia. 22, *Acrolophus ochraceus*, ventral view. 23, *A. triatomellus*, ventral view. All scales = 0.5 mm.

***Urodus mirella* (Möschler)**

Figs. 6, 20–21

Pexicnemidia mirella Möschler, 1890: 338.—Walsingham, 1892: 518; 1897: 167.—

Forbes, 1930: 159.—Wolcott, 1951: 743.

Urodus mirella (Möschler).—Davis, in Heppner, 1984: 55.

Although no longer considered a member of Tineidae, some discussion of this taxon is required. Forbes (1930) first questioned the family placement of *Pexicnemidia*, suspecting it to be either a member of Psychidae or Yponomeutidae. Upon examining the holotype, the author immediately recognized the genus as a junior synonym of the rather large neotropical genus *Urodus* Herrich-Schäffer. In the recent Neotropical Checklist, Heppner (1984) provisionally places *Urodus* in the Yponomeutidae, where it has been relegated by most authors in this century. Kyrki (1984) removed *Urodus* from the Yponomeutoidea on the basis of several features of the adult and immatures, principal among which was the presence of a tortricoid abdominal articulation. Currently the genus is in limbo, unassigned to any superfamily.

Möschler described *P. mirella* from two males, both collected from undesig-nated locals in Puerto Rico. One of the specimens, bearing a lectotype label (by D. Davis) and a ♂ genitalia slide label (D. R. Davis, no. 3456), is hereby designated lectotype.

Urodus mirella is almost certainly a junior synonym of *U. sordidata* (Zeller, 1877). Because the present deposition of the unique male holotype of the latter

is unknown, their synonymy cannot be verified. Searches for the missing holotype in the collections of the BM(NH), NHMV, TMB, and ZMHB have been futile. *Urodus sordidata* is approximately the same size and color of *U. mirella* and, similarly, was described from Puerto Rico. Among its diagnostic features, Zeller mentions the prominent black hairpencil present at the base of 1A on the dorsum of the male hindwings. This hairpencil is also present of the lectotype of *U. mirella* (see Fig. 6).

In addition to the Puerto Rican material examined, I have also collected this species from the Dominican Republic, where I found both *mirella* and a closely allied species at various sites but mostly around the Central Cordillera. The second species, with distinctly different male genitalia and darker hindwings than *U. mirella*, is identical to USNM material from Cuba which is believed to represent *U. ovata* (Zeller).

Additional material examined: DOMINICAN REPUBLIC: Dajabon Prov: 13 km S Loma de Cabrera, ca 400 m: 1 ♂, 20–22 May. El Seibo Prov: 15 km S Milches, ca. 500 m: 1 ♂, 1 ♀, 31 May. La Estrellata Prov: 4 km SE Rio Limpio, ca. 760 m: 1 ♀, 24–25 May. La Vega Prov: Constanza, Hotel Nueva Suiza, 1164 m: 1 ♀, 29 May. 10 km NE Jarabacoa, Hotel Montaña, ca. 520 m: 3 ♂, 1 ♀, 28 May. La Palma, 12 km E El Rio: 2–13 June. PUERTO RICO: Cialitos Cruces, 7 km S Ciales, 3200 ft (976 m): 1 ♂, 1 ♀, 2 Feb.–12 Mar. Maricao State Forest: 2 ♂, 29 July. San German: 1 ♂, 12–22 Feb. All specimens deposited in USNM.

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I thank H. J. Hannemann (ZMHB), F. Kasy (NHMV), A. Popescu-Gorj (MGAB), and G. Robinson (BMNH) for loans or information regarding pertinent type material in collections under their care. I am indebted to my former assistant Biruta Akersberg Hansen and to my present assistant Vichai Malikul for the line drawings and to Victor Krantz of the Smithsonian Photographic Laboratory for the photographs. Silver West of our Department typed the final draft of the manuscript, which was reviewed by J. F. Gates Clarke. Collection of the Guana Island specimens was by S. Miller and supported by the Conservation Agency through a grant from the Mocatta Metals Corporation.

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**TWO NEW SPECIES OF *QUADRACEPS*
(MALLOPHAGA: PHILOPTERIDAE) FROM AUSTRALIA**

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Abstract.—Two new species of *Quadraceps* from Australia are described and illustrated: *Q. australis* off *Vanellus tricolor* and *Q. neoaustralis* off *Peltohyas australis*.

The avian family Charadriidae (Charadriiformes) contains at least 64 species of lapwings, plovers, killdeers, and dotterels. The Mallophaga normally found on these hosts are the amblyceran genera *Actornithophilus* Ferris and *Austromenopon* Bedford and the ischnoceran genera *Quadraceps* Clay and Meinertzhagen and *Saemundsson* Timmermann. Several bird species have two species of *Quadraceps* and there are no records of *Quadraceps* from 23 species of these birds. The two species of *Quadraceps* herewith described and illustrated will reduce to 21 the hosts which warrant special collecting efforts.

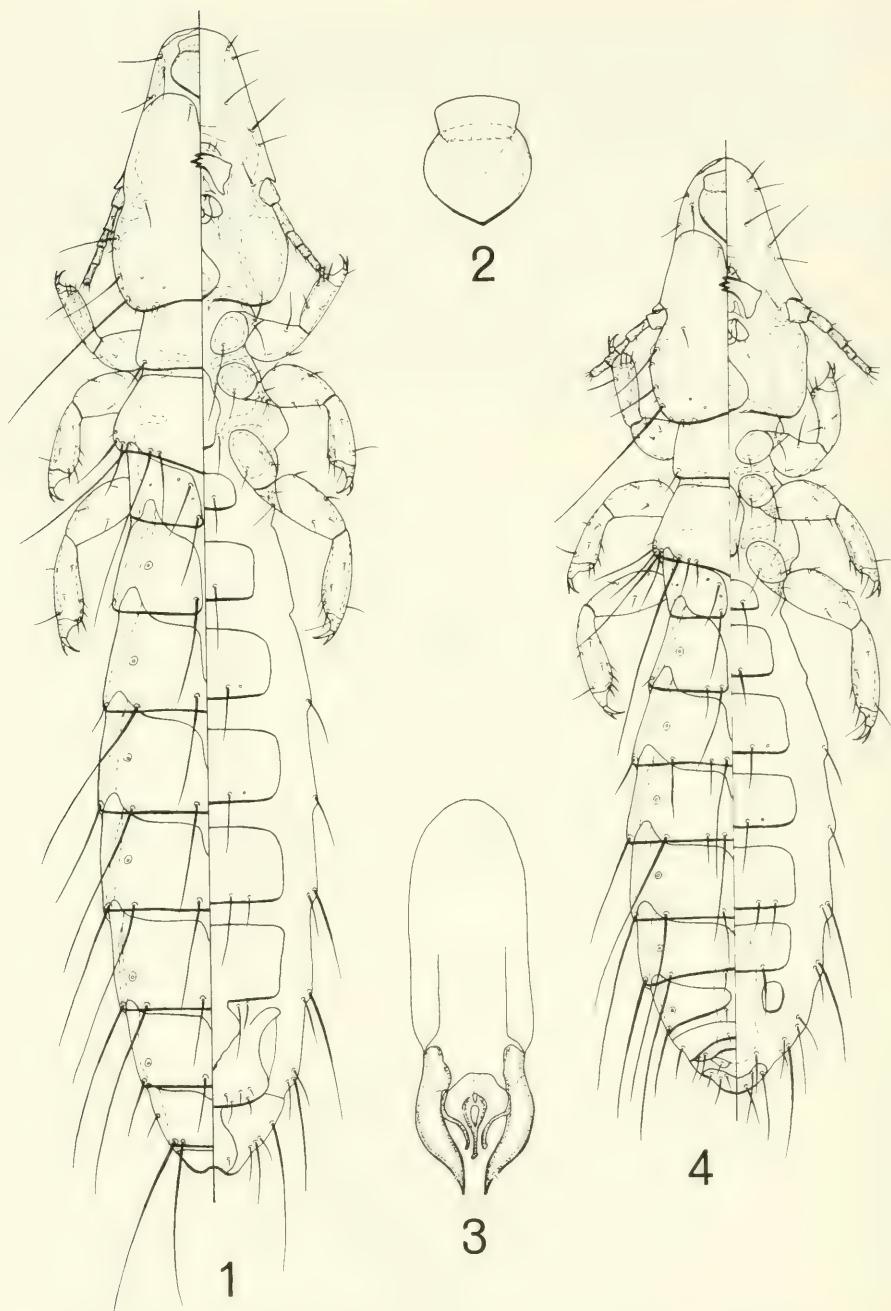
In the following descriptions, all measurements are in millimeters. The scientific names of the hosts are from Peters (1934). Paratypes of the new species will be distributed to the collections at the South Australian Museum, the National Museum of Natural History, Washington, D.C., the University of Minnesota, and Oklahoma State University.

***Quadraceps australis* Emerson and Price, NEW SPECIES**

Figs. 1-4

Type-host: *Vanellus tricolor* Horsfield, the Banded Plover.

Male.—External morphology and chaetotaxy as in Fig. 4. Head broadest across temples, with preantennal region tapered and evenly rounded; dorsal anterior plate (Fig. 2) heart-shaped with slightly convex anterior margin; temple margin on each side with 1 very long and 2 shorter setae; antennae essentially filiform, but with somewhat enlarged basal segment and elongated second segment; temple width, 0.26–0.27; head length, 0.42–0.43. Pronotum with 1 medium seta at each lateroposterior corner; each side of pteronotum with 8 setae, including 2 very long setae; pronotum width, 0.18–0.19; pteronotum width, 0.26–0.27. Abdomen with tergite II (first apparent tergite) and III completely divided at midline, IV–VII deeply to shallowly indented medioanteriorly, VIII narrowed and divided medially, and IX evenly narrowed. Marginal tergal setae: II, 2; III, 6; IV–V, 8; VI–VII, 6; VIII, 4; with lengths and distributions as shown in Fig. 4. Sternal setae: II–V, 2; VI, 4; VII, 2; dorsal and ventral terminalia as shown, without long dorsal setae. Abdomen width, 0.34–0.36; total body length, 1.54–1.58. Genitalia (Fig.



Figs. 1-4. *Quadriceps australis*. 1, Female. 2, Female dorsal anterior head plate. 3, Male genitalia. 4, Male.

3) with basal plate longer than parameres; parameres stout, inwardly curved and pointed posteriorly, with subapical minute seta; mesosomal structures as shown; genitalia length, 0.21–0.23; genitalia width, 0.07–0.08.

Female.—External morphology and chaetotaxy as in Fig. 1. Much as for male, except as follows. Temple width, 0.29–0.30; head length, 0.44–0.46. Each side of pteronotum with only 6 setae; pronotum width, 0.20; pteronotum width, 0.28–0.30. Tergite VIII much wider, with shallow medioanterior indentation; tergite IX also wider. Marginal tergal setae: III, 4; IV–V, 6. Sternite VII with 4 setae. Dorsal and ventral terminalia as shown, with tergite IX having 2 very long setae on each lateroposterior corner; each side of last segment evenly rounded. Abdomen width, 0.38–0.40; total body length, 1.92–1.95.

Discussion.—This species resembles *Q. renschi* Timmermann, 1954, found on *Vanellus miles* (Boddaert), the Masked Plover, that occurs in New Guinea and Australia; however, the two species have distinct differences. Both sexes of *Q. australis* are smaller than for *Q. renschi*. The female subgenital plate of these two species has a different shape. The endomeres of the male genitalia of *Q. renschi* are straight, whereas they are curved for *Q. australis*. The type-host of *Q. renschi* as given in the original description by Timmermann (1954) was "*Lobibyx novaehollandiae*," which most ornithologists now consider to be *Vanellus miles novaehollandiae* (Stephens).

Material examined.—Holotype ♂ from *Vanellus tricolor* collected in 1983 at Kimba, South Australia, by J. Little (B-37571); in the South Australian Museum. Paratypes: 7 ♂, 10 ♀, same data as holotype.

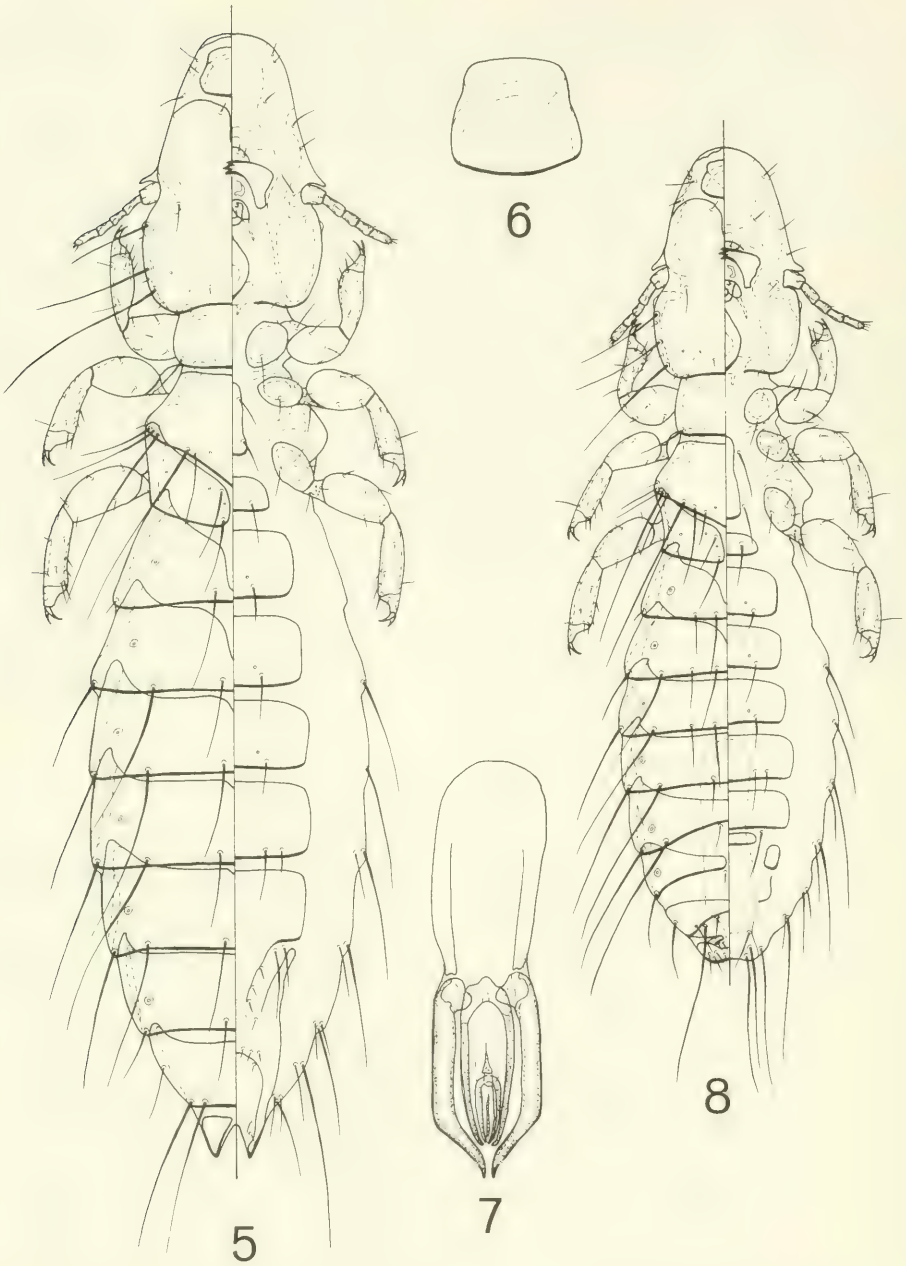
***Quadriceps neoaustralis* Emerson and Price, NEW SPECIES**

Figs. 5–8

Type-host: Peltodyas australis (Gould), the Australian Dotterel.

Male.—External morphology and chaetotaxy as in Fig. 8. Head broadest across temples, with preantennal region tapered and evenly rounded; dorsal anterior plate (Fig. 6) subtrapezoidal, with flattened to slightly convex anterior and posterior margins; temple margin on each side with 3 long to very long setae; antennae essentially filiform, with somewhat enlarged basal segment; temple width, 0.25–0.27; head length, 0.39–0.41. Pronotum and pteronotum as for *Q. australis*; pronotum width, 0.18–0.19; pteronotum width, 0.26–0.28. Abdomen with tergite II completely divided at midline, III–IV deeply to shallowly indented at midline, V–VI not indented and evenly wide across segment, VII narrowed and not indented, VIII narrowed and divided at midline, and IX undivided and narrowed toward midline. Marginal tergal setae: II, 2; III, 6; IV–V, 8; VI–VII, 6; VIII, 4; with lengths and distributions as shown. Sternal setae: II–V, 2; VI, 4; VII, 2; dorsal and ventral terminalia as shown, with very long seta associated with posterior margin of tergite IX and 3 very long setae on each side of ventral posterior margin. Abdomen width, 0.36–0.39; total body length, 1.40–1.43. Genitalia (Fig. 7) with basal plate about length of parameres; parameres parallel along basal two-thirds, abruptly bent inward posteriorly and pointed, with subapical minute seta; mesosomal structures elongate, as shown; genitalia length, 0.35–0.37; genitalia width, 0.09–0.10.

Female.—External morphology and chaetotaxy as in Fig. 5. Much as for male,



Figs. 5-8. *Quadraceps neoaustralis*. 5, Female. 6, Female dorsal anterior head plate. 7, Male genitalia. 8, Male.

except as follows. Temple width, 0.30–0.31; head length, 0.44–0.46. Each side of pteronotum with only 6 setae; pronotum width, 0.20–0.21; pteronotum width, 0.30–0.33. Abdomen with tergites III–VII deeply to shallowly indented medioanteriorly; VIII–IX undivided and equally wide across segment. Marginal tergal setae: III, 4; IV–V, 6. Dorsal and ventral terminalia as shown, with tergite IX having 2 very long setae at each lateroposterior corner; ventrally with elongate series of short setae; each side of last segment pointed, bearing triangular dorsal sclerite. Abdomen width, 0.45–0.49; total body length, 1.78–1.92.

Discussion.—*Quadriceps neoaustralis* is related to the *Q. fissus* (Burmeister, 1838)–*Q. assimilis* (Piaget, 1890) complexes found on avian hosts of the genus *Charadrius* and related genera (Timmermann, 1954 and 1957). However, both sexes of *Q. neoaustralis* are smaller than for the related taxa. In the female of *Q. neoaustralis*, the indented tergites III–VII are unique, as are the shape of the tergal plates on VII–IX. In the male of this species, the sternal and tergal plates on VII–IX are unique, as are also the long slender tapered gently curved genitalic endomeres and the long basal plate.

Material examined.—Holotype ♂ from *Peltohyas australis* collected on July 22, 1984, at Dulkaninna, South Australia, by J. M. Bourne (B-38426); in the South Australian Museum. Paratypes: 4 ♂, 8 ♀, same data as holotype; 1 ♀, same except collected May 19, 1984, at 15 km S. of Burra, South Australia, by J. M. Bourne (B-37975).

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NEOTROPICAL TINEIDAE, II: BIOLOGICAL NOTES AND
DESCRIPTIONS OF TWO NEW MOTHS PHORETIC ON
SPINY POCKET MICE IN COSTA RICA
(LEPIDOPTERA: TINEOIDEA)

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Abstract.—Two new species of tineid moths discovered riding on the backs of two species of spiny pocket mice (Heteromyidae) in Costa Rica are described. *Amydria selvae*, new species, was found on *Heteromys desmarestianus* Gray in the rainforest at Finca La Selva and *Ptilopsaltis santarosae*, new species, occurred on *Liomys salvini* (Thomas) in the dry forest at Santa Rosa National Park. Only female moths were observed and collected. Biological observations on both moths and their hosts in phoresy are summarized.

Recent live-trapping of spiny pocket mice in Costa Rican forests has revealed the association of three species of phoretic moths of the family Tineidae. The life histories of the moths are still poorly understood and only the females are known to be phoretic. No males of any of the three species have been discovered. Excavations of the burrows of the two species of spiny mice are now underway, which we hope will reveal not only the presence of males with associated immatures but also the larval biology.

All moths (females) were collected from the backs of two species of mice from two quite different localities. In the drier, deciduous forest habitat of Santa Rosa National Park, a new species of *Ptilopsaltis* was found on *Liomys salvini* (Thomas). At the wetter, evergreen forest habitat of La Selva, two species of Tineidae were collected from the backs of *Heteromys desmarestianus* Gray. One of these, *Amydria selvae*, new species, is described herein. The other, apparently another undescribed *Ptilopsaltis* quite distinct from the one at Santa Rosa, has not been named due to inadequate material.

Comparison of these "mouse moths" with the well known sloth moths (Waage and Montgomery, 1976) is inevitable, although much of the life history of the former is still conjecture. Of the 16 species now recognized in the exclusively American genus *Amydria*, food preferences of only two have been noted. Johnson and Martin (1969) report larvae of *A. effrentella* Clemens feeding on dried plant

(nest) material in mountain beaver burrows. Populations of *A. arizonella* Dietz have been commonly observed by the senior author in numerous bat caves throughout southwestern United States, where the larvae burrow and feed in bat guano (Davis, 1972). From these two accounts, it is likely that *A. selvae* will prove to be a scavenger within the nests of *H. desmarestianus*, either on mouse dung or on plant debris, with the latter most probable.

Even though the neotropical genus *Ptilopsaltis* is reportedly monotypic (type = *P. synchorista* Meyrick, Fig. 4) and known only from Trinidad (Davis, 1984), the senior author knows of at least five other species ranging from the southwestern United States to Venezuela, in addition to the two mentioned in the present paper. Little has been published previously on the food habits of *Ptilopsaltis*, although specimen labels on *P. synchorista* Meyrick in the BMNH state "larva feeding on seeds disgorged by Guacharo bird on floor of limestone cave" in Trinidad. This suggests that *P. santarosae*, new species, may also feed on plant debris in the nests of *Liomys salvini*.

The pretarsi of both species of mouse moths were examined by the senior author in search of special adaptations for clinging to the hairs of their hosts. The results were somewhat inconclusive and will be discussed further in a future revision of the genus *Ptilopsaltis*. All pretarsi of female *Amydria selvae* are similar with little modification except for the disorientation of one tarsal claw on the fore- and midlegs (Fig. 11). The pretarsi of female *Ptilopsaltis santarosae* are much more modified with one tarsal claw disoriented and one pulvillus reduced on the fore- and midlegs (Fig. 13). The hind-pretarsi are even more specialized with elongate but symmetrical claws and greatly reduced arolium (Figs. 15, 16). Examinations of other *Ptilopsaltis* species show similar pretarsal specializations in both males and females.

Deposition of specimens referred to in this paper are as follows: BMNH, for British Museum (Natural History), London, England; MNCR, Museo Nacional de Costa Rica, San Jose, Costa Rica; UCB, University of California, Berkeley, California; and USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C.

Amydria selvae Davis, NEW SPECIES

Figs. 1, 5, 7, 11–12

Adult (Fig. 1).—Length of forewing: ♀, 5–6 mm. A relatively small species with pale buff to cream colored body and forewings, possessing a few brownish fuscous spots around margin of wing. Male unknown.

Head: Vestiture rough on vertex, relatively smooth on frons, uniformly cream colored except for lateral patches of fuscous on frons near margin of eye. Antennae approximately 0.6 the length of forewing, 54–59 segmented; scape mostly pale buff to cream with anterior margin fuscous; pecten absent; flagellum uniformly cream; smooth. Maxillary palpi greatly reduced, 1 minute segment. Labial palpi mostly pale buff to cream with latero-ventral surfaces of I and basal half of II fuscous; II also with 3–4 dark bristles laterally.

Thorax: Pronotum pale buff to cream. Tegulae with fuscous on anterior margin. Venter cream to white. Forewings pale buff to cream, nearly immaculate except for 2–3 small costal spots, 4–5 extremely small subterminal spots and one mod-



Figs. 1-4. Adult moths. 1, *Amydria selvae*, ♀ holotype, forewing length 6 mm. 2, *A. pauculella*, ♀ holotype, forewing length 8 mm. 3, *Ptilopsaltis santarosae*, ♀ holotype, forewing length 10 mm. 4, *P. synchorista*, ♂ holotype, forewing length 7 mm.

erately large subternal spot; all markings dark brownish fuscous; fringes pale buff to cream. Hindwings uniformly whitish cream, slightly whiter than forewings. Forelegs pale buff to cream ventrally, brownish fuscous dorsally with apices of tibiae and tarsal segment, and entire pretarsus suffused with pale buff; arolium and pulvilli well developed on all legs. Midlegs mostly cream ventrally, brownish fuscous dorsally with apices of tarsal segments and entire pretarsus suffused with pale buff. Hindlegs predominantly cream to white, dorsal surfaces of outer four tarsal segments gray with pale buff suffusion at apices.

Abdomen: Uniformly pale buff.

Female genitalia: As shown in Fig. 7. Ovipositor extremely short, moderately broad. Posterior apophyses short; anterior apophyses absent. Ostium relatively simple, flush with body wall. Caudal half of ductus bursae slightly enlarged and thickened to form a distinct antrum; ductus then narrowing to a slender, short tube to corpus bursae. Corpus bursae with a relatively slender lobe arising from caudal end near junction with ductus bursae. Signum absent.

Immature stages.—Unknown.

Holotype.—♀. Finca La Selva Biological Station, near Puerto Viejo de Sarapiquí, Heredia Province, Costa Rica; 13 July 1984, coll. A. P. Brooke, ex ♂ *Heteromys*, trap no. 4 (UCB).

Paratypes.—Same locality as holotype: 1 ♀, 5 July 1984, D. H. Clayton; 1 ♀, 8 July 1984, D. H. Clayton; 2 ♀, 20 July 1984, ♀ 41 E4, A. P. Brooke; 1 ♀, 23 July 1984, E 1 on no. 0003, A. P. Brooke. Paratypes deposited in MNCR, UCB, USNM.

Host.—Larval substrate unknown; adult females collected riding on live *Heteromys desmarestianus* Gray.

Flight period.—July.

Distribution.—Known only from the type locality, which is a lowland evergreen rainforest site (ca. 100 m) located one km upstream from Puerto Viejo de Sarapiquí, Finca La Selva Biological Station, Heredia Province, Costa Rica.

Etymology.—The specific epithet is derived from the general type locality (La Selva) of the species.

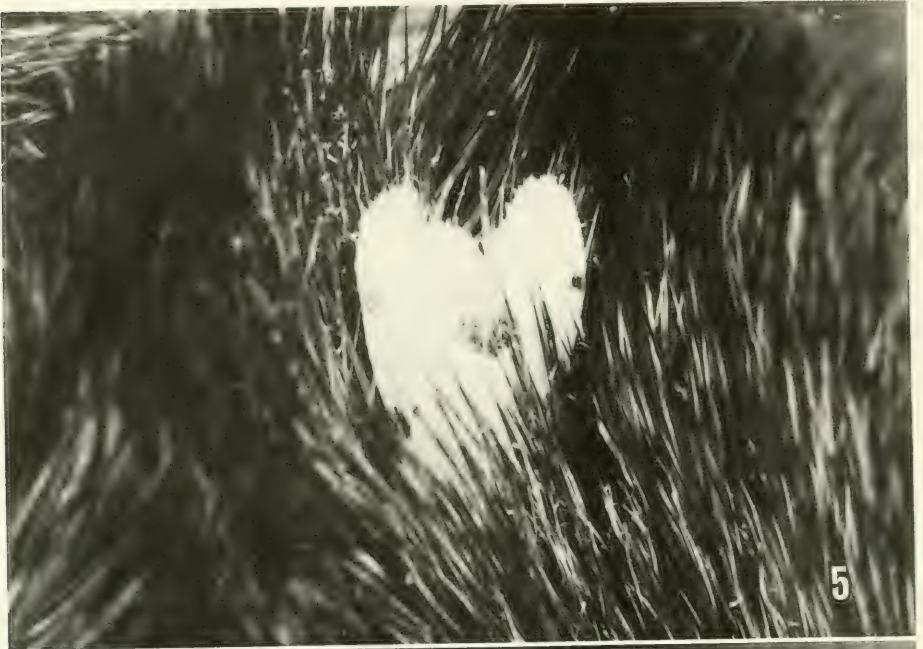
Discussion.—*Amydria selvae* most closely resembles *A. pauculella* (Walker) known only by the female type from Venezuela. Both species possess pale buff forewings with a few dark spots bordering the wing margins. The forewings of female *A. pauculella* (Fig. 2) are slightly larger, measuring 8 mm in length compared to 5 to 6 mm for *A. selvae*. The most diagnostic features distinguishing the females of the two species are the relative development of the sterigma (see Figs. 7–8), ductus bursae, and accessory bursae. Walsingham (1914) mistakenly records *A. pauculella* from Costa Rica. His material, from Volcan de Irazu, actually represents an undescribed species of *Amydria*.

Biological observations.—*Amydria selvae* were collected from *Heteromys desmarestianus* Gray captured in Tomahawk live-traps at Finca La Selva (10°30'N, 84°00'W), a lowland (ca. 100 m) wet forest site one km upstream from Puerto Viejo de Sarapiquí, Prov. Heredia, Costa Rica. Traps were baited with corn and set in a grid covering several hectares of an overgrown cacao (*Theobroma cacao*) plantation. *H. desmarestianus* is a locally abundant heteromyid rodent inhabiting montane or tropical rain forests of Mexico, Costa Rica, and Panama. It is primarily granivorous and collects seeds in external cheek pouches, later storing them in underground burrow systems. Adult males average 83 g and females 62 g (Fleming, 1974).

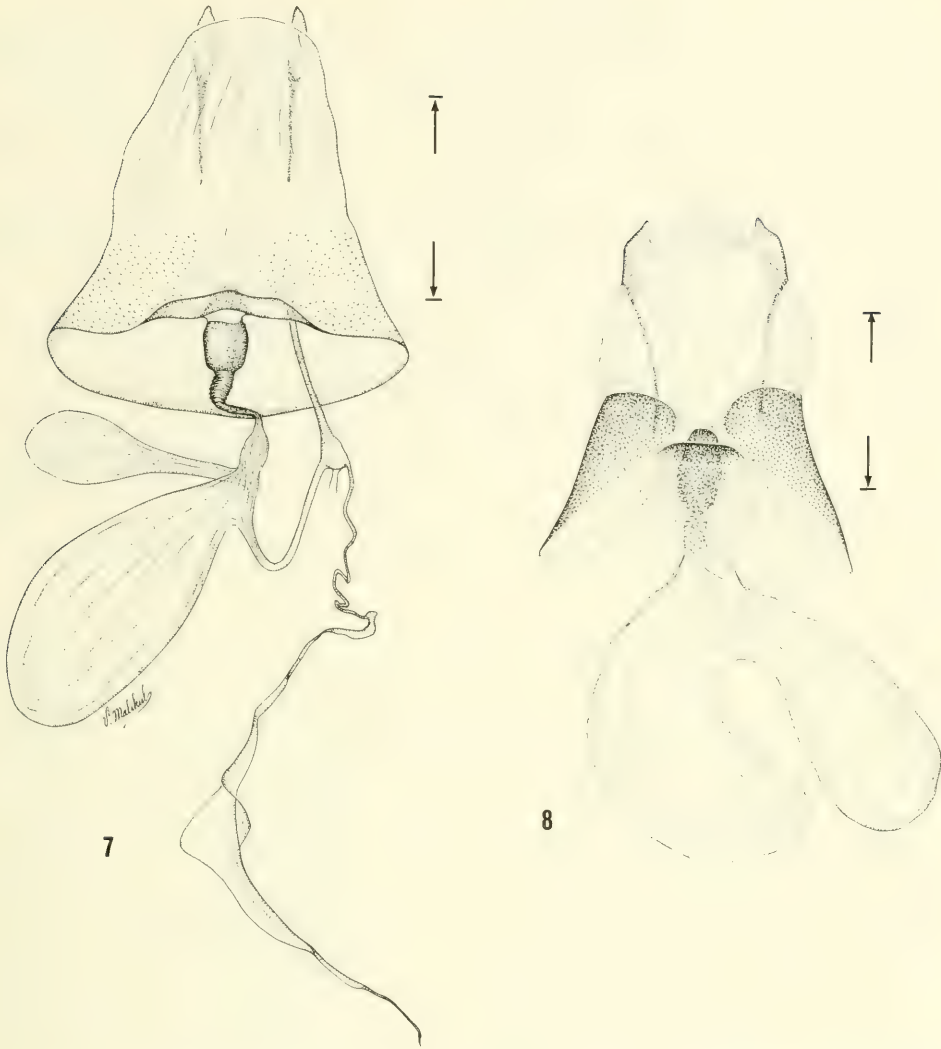
A total of 58 *H. desmarestianus* (female: male = 2:5) was trapped nocturnally throughout July, 1984 and examined for moths the following morning. Ten female moths were collected from six *H. desmarestianus* (two adult males, three adult females, and one female, age unknown). Five additional moths were observed on mice, but flew before capture. Male mice carried four moths apiece; three females carried two apiece and a fourth female (adult) carried one moth. One adult female first captured with no moths was recaptured several days later carrying two moths. Another adult female from which two moths were removed at first capture was recaptured eight days later with no moths.

Moths were not collected from any of 50 additional *H. desmarestianus* trapped in other lowland and highland areas of Costa Rica during July–August, 1984. Furthermore, during an intensive trapping campaign of three weeks at Finca La Selva in late August and September, no moths were observed on any of 160 individually marked *H. desmarestianus*.

Most moths were observed on the rumps of mice, either on the surface of the



Figs. 5, 6. Live female mouse moths in situ on backs of hosts. 5, *Amydria selvae* embedded in the fur of *Heteromys desmarestianus*. 6, *Ptilopsaltis santarosae* riding motionless on the back of *Liomys salvini*.



Figs. 7, 8. Female genitalia, ventral view. 7, *Amydria selvae*. 8, *A. pauculella*. (Scales = 0.5 mm.)

pelage or embedded in it with only the tips of the wings and abdomen exposed (Fig. 5). One moth was collected from the shoulder of a mouse and another was collected from the tail of another mouse. Except for the tail, these regions are well protected from host grooming, a major source of mortality for arthropod associates of vertebrates (Marshall, 1981). Bell and Clifford (1964) demonstrated the importance of allogrooming (grooming of one individual by another) between the sexes for the control of ectoparasites on mice. It would be interesting to know whether there is any impact of grooming and allogrooming on mouse moths. The wings of some moths were tattered, perhaps due to host grooming or abrasion against the spiny pelage of *H. desmarestianus*.

Mouse moths are capable of enduring considerable activity on the part of the

host. In one case, a moth remained on its mouse for well over an hour as the mouse, an escapee, was chased wildly about the laboratory. When placed in a petri dish in the lab, moths were capable of rapid locomotion, preferring the curved sides of the dish to its flat, but more exposed, top or bottom. Assisted by the presence of arolia on the hindlegs, moths were able to walk vertically and upside down on plastic and glass surfaces.

Waage (1979) distinguished two general types of association between Lepidoptera and vertebrates: "those involving prolonged adult association with the host and larval dependence on the host's microhabitat, and those involving only brief adult feeding associations and no larval dependence."

We have not observed reproduction in *Amydria selvae*. However, closely related species are known to fit Waage's first category of association. Johnson and Martin (1969) collected more than 300 *A. effrentella* from each of several nests of mountain beavers (*Aplodontia rufa*). Both adults and larvae were found in the nests, where the larvae fed on decaying vegetation. Davis (1972) reported the larvae of *A. arizonella* burrowing in the accumulated bat guano of caves. Jellison (1940) noted that species of several tineid genera were common inhabitants of the nests of various mammals and birds. He considered *Amydria* sp. to be a regular associate in the nests of burrowing owls (*Speotyto cunicularia*) and pocket gophers (*Geomys floridanus*).

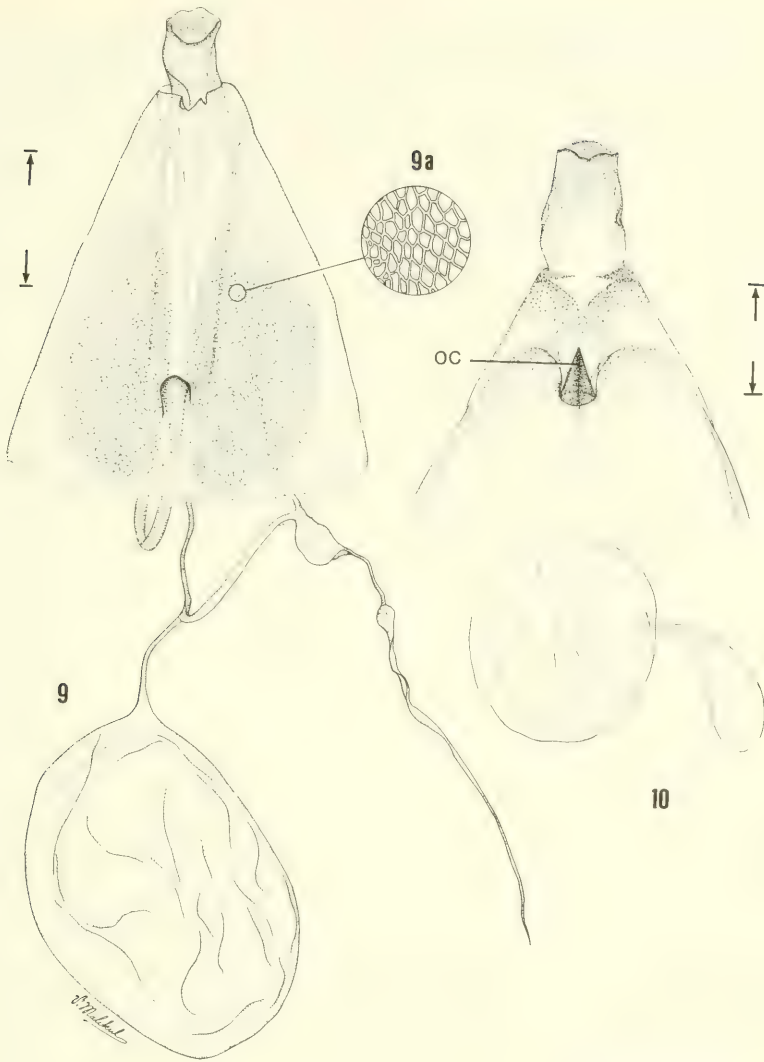
The fact that we collected only females of *A. selvae* or *Ptilopsaltis santarosae* (see below) is a striking departure from the other documented case of moths that are phoretic on mammals: "The continuous, phoretic association of female moths with sloths facilitates the location of fresh dung piles for oviposition. In *Cryptoses choloepi* Dyar in Panama, males are three to four times as common (on) sloths as females, although the primary sex ratio is about one to one (Waage and Montgomery, 1976). Perhaps this reflects the tendency of males to remain and accumulate on sloths in order to compete for newly-arriving females, in contrast to a regular loss of females from the host population at each defecation by the host." (Waage, 1979). Because oviposition and the early developmental stages of *A. selvae* presumably occur in the nest of *H. desmarestianus*, phoresis most likely serves as a temporary means of dispersal among nests for females in search of new oviposition sites. Knowledge of the primary sex ratio for *A. selvae* must await the collection of more material, probably via the excavation of burrows.

Ptilopsaltis santarosae Davis, NEW SPECIES

Figs. 3, 6, 9, 13-16

Adult (Fig. 3).—Length of forewing: ♀, 8–9.5 mm. A moderately large moth with light buff forewings marked with numerous, scattered dark brownish fuscous spots of various sizes. Male unknown.

Head: Vestiture of vertex light to medium brown; frons mostly cream to white with a patch of medium brown scales arising near base of frons and inner rim of eye. Antennae approximately 0.8 the length of forewing, 79–86 segmented; scape smooth, without pecten, uniformly light buff; flagellum uniformly stramineous, nearly white at apex. Maxillary palpi extremely reduced, less than 0.5 the length of labial palpus I, 3-segmented, basal segment nearly sessile; vestiture light brown to buff. Labial palpi well developed 3-segmented; vestiture light brown, becoming



Figs. 9, 10. Female genitalia, ventral view. 9, *Ptilopsaltis santarosae*. 9a, Detail of surface of eighth sternite. 10, *P.* species, OC = ostial cone. (Scales = 0.5 mm.)

pale buff to nearly white on segment III; II with a prominent ventral brush and 2–3 dark bristle-like setae laterally; vestiture of III smooth.

Thorax: Pronotum mostly light brown with darker brown on anterior edge of tegulae. Venter predominantly white. Forewings light buff with dark, brownish fuscous spots scattered over dorsal surface; spots most noticeable along costa, with a relative large, oblique spot at apex of discal cell and another near base of forewings; fringes light buff. Hindwings uniformly pale silvery gray. Forelegs with coxa and femur pale buff; tibia and tarsal segments brownish fuscous dorsally, with apices light buff, whitish ventrally; pretarsi with one pulvillus greatly reduced;

pseudempodial seta reduced; arolium normal. Midlegs mostly light buff; tibia and tarsi only slightly darker dorsally; pretarsi with one pulvillus and pseudempodial seta reduced as in forelegs. Hindlegs mostly whitish; tibia and tarsi light buff dorsally; pretarsi with arolium and pseudempodial setae greatly reduced, pulvilli symmetrical, claws elongate and only slightly curved.

Abdomen: Light buff.

Female genitalia: As shown in Fig. 9. Ovipositor extremely short, slender. Anterior apophyses absent. Eighth sternite enlarged, approximately twice the length of 8T, with a large pair of ovoid, lightly sclerotized plates bearing a finely reticulate surface (Fig. 9a); ostial cone greatly reduced, apex rounded, barely rising from 8S, opening of ostium situated at anterior third of 8S. Ductus bursae slender but larger than any other species of *Ptilopsaltis*, becoming more slender toward juncture with corpus bursae; corpus bursae nearly round; signum absent.

Immature stages.—Unknown.

Holotype.—♀. Santa Rosa National Park, 25 km S of La Cruz, Guanacaste Province, Costa Rica; 22 May 1983, coll. D. H. Janzen, USNM type no. 100673 (USNM).

Paratypes.—Costa Rica: Same locality as holotype: 3 ♀, 12 May 1984; 1 ♀, 14 May 1984; 2 ♀, 22 May 1983; 1 ♀, 5 Aug. 1984. Paratypes deposited in BMNH, MNCR and USNM.

Host.—Larval substrate unknown; adult females collected from fur of live *Liomys salvini*.

Flight period.—May, August.

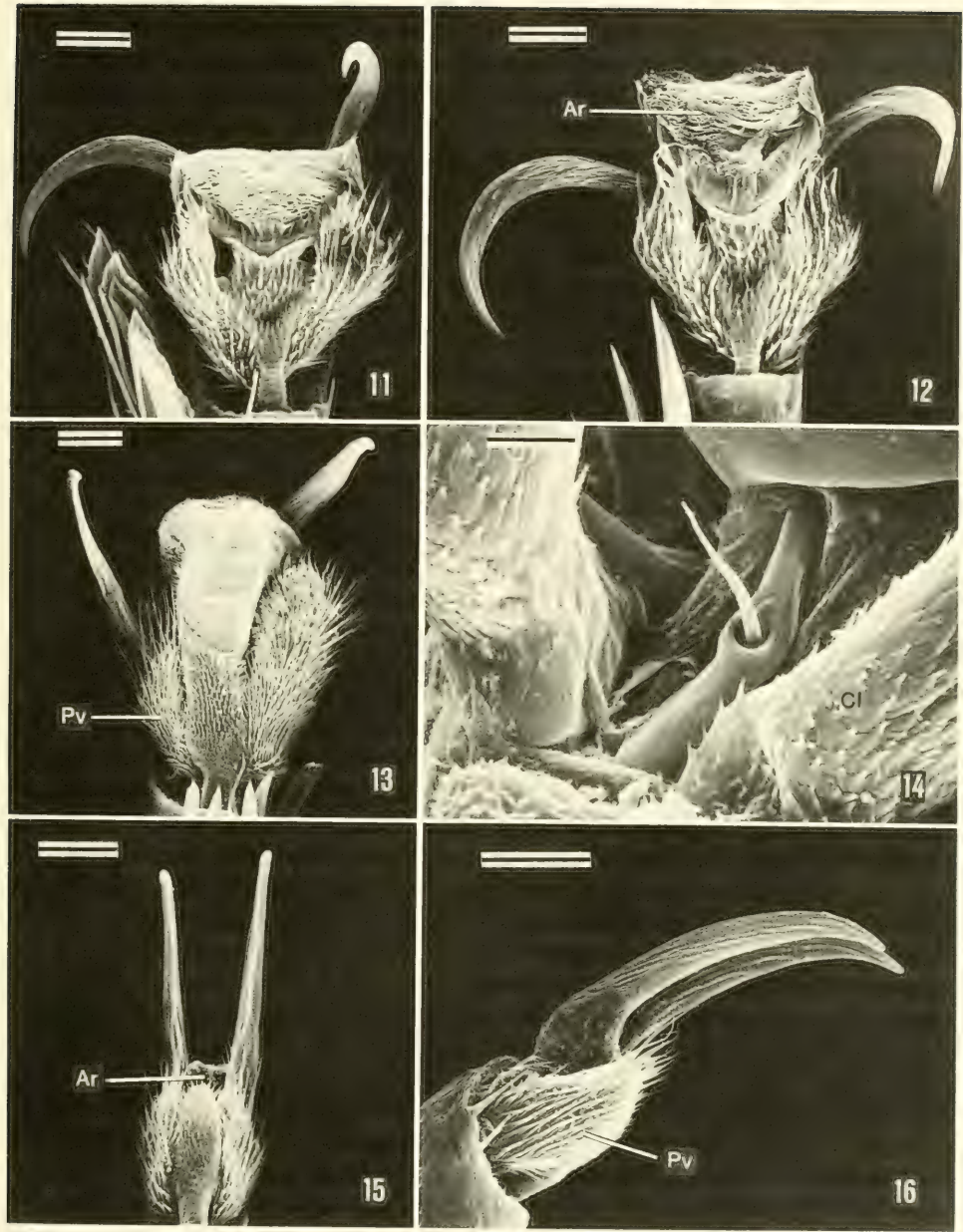
Distribution.—Known only from the type locality, which is a lowland deciduous forest site (ca. 250–300 m) in Santa Rosa National Park, 25 km south of La Cruz in the northwest corner of Guanacaste Province, Costa Rica.

Etymology.—The species name is derived from the type locality (Santa Rosa).

Discussion.—Of the several species of *Ptilopsaltis* known (but mostly unnamed), the female of this species is unique in having the ostial cone greatly reduced and rounded. In all other species, this structure is decidedly conical in form and often strongly attenuated. Another apomorphy of *P. santarosae* is the presence of a pair of nearly contiguous, finely reticulated, ovoid areas on the eighth sternite (Fig. 9a).

A second species of *Ptilopsaltis* has been collected on *Heteromys desmarestianus* at La Selva. Although superficially similar in appearance (as are most members of this genus) the two species are easily differentiated by their characteristic female genitalia (Figs. 9, 10). Description of the La Selva species will have to await the collection of more suitable type material.

Biological observations.—All specimens of *Ptilopsaltis santarosae* were collected while they were riding on the dorsum of *Liomys salvini* (Thomas) in Santa Rosa National Park, 25 km south of La Cruz, northwestern Guanacaste Province, Costa Rica. *L. salvini* is a 20–70 g heteromyid mouse that is active as a seed collector on forest litter at night (Janzen, 1982). While the actual collection dates were 22 May 1982, 12–14 May 1984, and 5 August 1984, other moths were observed on the mice in all other months of the year (1981–1984). The mice were trapped in *Enterolobium* seed-baited Sherman live traps during the night, and



Figs. 11–16. Pretarsal morphology. 11, *Amydria selvae*, midleg, ventral view (scale = 20 μ m). 12, Hindleg (Ar = arolium; scale = 20 μ m). 13, *Ptilopsaltis santarosae*, midleg (Pv = pulvillus; scale = 40 μ m). 14, Pseudempodial seta between bases of claws, dorsal view (Cl = claw; scale = 10 μ m). 15, Hindleg, ventral view (Ar = arolium; scale = 40 μ m). 16, Hindleg, lateral view (Pv = pulvillus; scale = 40 μ m).

removed between 0700 and 1100 hours. If the mouse was not roughly handled, the moth remained motionless while clinging tightly to the surface of fur just above the base of the tail (dorsally) or in the center of the back just behind the head (Fig. 6). If the mouse was dumped into a plastic bag and jumped about frantically, the moth often flew off. However, if the moth and mouse were then left together in the bag, the moth quickly again assumed a stationary position on the mouse. If the moth was freed from the plastic bag, it flew a few tens of centimeters and then perched motionless on a solid substrate.

Moths were taken off of *L. salvini* of both sexes, ranging from 18 g youngsters (probably foraging from their mother's nest) to 50–70 g fully reproductive adults. In nine cases, there was a single moth per mouse, and in one case there were two moths, riding side by side. All eleven moths collected were females. Presumably these moths were dispersing among nests by riding on the mice. This suggests that the mice occasionally enter each other's burrow systems or even nests. However, the information gathered to date suggests that *L. salvini* normally exist at a density of one adult per nest or even burrow system (see Fleming, 1983).

At Santa Rosa, the moths were collected from mice in pristine, nearly evergreen forest (Bosque Humedo Mouse Plot) and in 60 to 90-year-old secondary successional vegetation (San Emilio Mouse Plot). Small moths, presumably *P. santarosae*, were noticed riding on *L. salvini* taken in live traps in late successional secondary deciduous forest in Finca La Pacifica, 7 km north of Canas, Guanacaste province, Costa Rica (T. H. Fleming, personal communication).

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A NEW CRYPTIC SPECIES OF *ODONTOLOXOZUS*
(NERIIDAE:DIPTERA) FROM THE CAPE REGION OF
BAJA CALIFORNIA SUR (MEXICO)

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Abstract. — A new species of *Odontoloxozus* was discovered from the cape region of Baja California Sur. Differences between *O. pachycticola* n. sp. and *O. longicornis* Coquillett are described for adult and larval morphology, cytology and mating behavior. The two species hybridize readily in the laboratory and produce sterile hybrids. Differences in chromosome number, translocations, inversions and differences in degree of ectopic pairing of salivary chromosomes distinguish the species cytologically. Adults may be distinguished by differences in numbers of anepisternal spots, larvae differ in numbers of papillae on anterior spiracles. In analysis of copulation times for intra- and interspecific crosses, hybrids demonstrated clear reproductive differences in the species.

Closely related and morphologically similar species have been called cryptic species. Studies of these species have frequently produced interesting and useful information concerning population genetics and behavior as they interact in the processes of evolution. Reproductive isolation and the resulting integrity of gene pools may result from numerous combinations of genetic and ecological factors (Bush, 1975). While sibling or cryptic species may present serious problems to taxonomists, the value of these taxa to systematic zoology has been shown to be extensive (e.g. Dobzhansky and Epling, 1944; White, 1973).

In this study we describe *Odontoloxozus pachycticola* n. sp. based on evidence from adult and larval morphology, hybrid sterility, cytogenetics, and mating behavior. This last evidence was actually the first discovered during a study, following Mangan (1979), of the mating behavior of *O. longicornis* Coquillett in which males of *O. longicornis* were found to have difficulty mating with females from populations collected in the cape region of Baja California Sur, Mexico. We feel that evolution in this family is particularly interesting in that there are ecological and genetic parallels between these neriid species and better known species of the *nannoptera* and *repleta* species groups of *Drosophila* (Heed, 1982; Mangan, 1982) which co-inhabit cactus substrates with *Odontoloxozus* spp. (Mangan, 1984).

MATERIALS AND METHODS

Odontoloxozus longicornis adults used in this study were collected from three locations. Collections were made in the Tucson vicinity of Pima County, Arizona

by placing vials over males and females on saguaro cacti (*Carnegea gigantea* (Engelm.)) and by rearing larvae from infested necrotic limbs of the cactus. Adults from a coastal region north of Bahia Kino, Sonora were reared from necrotic sections of agria cactus (*Machaerocereus gummosus* (Engelm.)) and cardon cactus (*Pachycereus pringlei* (S. Wats.)). Mazatlan populations from Sinaloa were reared from necrotic sections of hecho cactus (*Pachycereus pectin-aborigium* (Engelm.)). These samples were all collected in mid-March of 1977 and 1978. Adults of *O. pachycericola* were reared from senita cactus (*Lophocereus schottii* (Engelm.)) and cardon cactus collected in March of the same years, further specimens were taken as adults from cactus stems and pinned during the 1978 collections.

Flies were maintained on *Drosophila* medium (banana, malt extract, yeast extract, agar) for several generations in population cages or in half pint milk bottles. This medium had to be periodically replenished (2 or 3 times in the 3–5 week development period). Dry tissue paper was inserted into the bottles to provide suitable pupation sites.

Third stage larvae and mature adults were examined for morphological characters to distinguish the populations. Larvae were softened for 20–24 hours in 30% KOH for removal of cephalopharyngeal skeleton and spiracles. Male genitalia were boiled in 30% KOH for 3–5 minutes before dissection. Differences between the species, and between the species and hybrids, were tested using appropriate “*t*” tests for comparisons of mean values after transformation in accordance with standard statistical procedures.

Third stage larvae were used for analysis of polytene chromosomes. Salivary glands were removed, fixed in sodium citrate (1%) then stained and squashed in acetic orcein. Karyotypes were determined from brain cells removed at the same time. These were also fixed in sodium citrate, then stained for 3 to 4 hours in acetic orcein and squashed. Testes were removed from male pupae or newly emerged adults in insect saline, teased apart, and stained in acetic orcein for 45 minutes.

Pair mating tests for production of hybrids and analysis of behavior were performed by placing 3 to 5 day old virgin males and females in 8 dram vials with *Drosophila* medium provided for adult nutrition. Mating times were recorded for at least 6 pairs when possible for each of the combinations of reciprocal crosses among the 4 collection locations. Due to lack of sufficient numbers of virgin flies of the same age, certain crosses could not be made. Slow development in the Tucson populations resulted in a shortage of females, while the Baja California Sur (La Paz) samples produced few males at the time the other groups were emerging. It was decided to test within site matings completely, then look at between site matings with emphasis on crosses between sites in which pairs showed extended mating times or populations had different karyotypes. Mating times were recorded using a stopwatch with time measured as period of genital contact. First and repeated matings were recorded for each pair for a period of 4 hours of observation.

RESULTS

Analysis of data and observations for comparisons of genetics and behavior of these four populations is divided into three sections. Morphological comparisons are given first, as these provide the basis for description of *O. pachycericola*. Adult

and larval stages of *O. longicornis* were described by Olsen and Ryckmann (1963); additional description of third stage larval characters was provided in Steyskal (1965). The description of *O. pachycticola* follows, then a description and comparison of the karyotypes and polytene configurations of the two species. The last section of results includes analysis of mating behavior for inter- and intra-population crosses.

Morphological comparisons and diagnoses. — Analysis of thoracic pigmentation (spot number) and third instar papilla number for both anterior spiracles (Table 1) allows separation of adults and third stage larvae of the species. Spots on the left anepisternum were used as this surface is small enough to provide a reasonable number of spots to count and is normally visible on mounted specimens. These data show that *O. longicornis* average about twice as many spots as *O. pachycticola*. Differences between species are highly significant (i.e. there is no overlap), and there is no significant variation among the 3 *O. longicornis* populations ($P > 0.5$). Spot number does not differ significantly between hybrids and *O. pachycticola* ($t = 1.73$, $P > 0.05$), indicating possible dominance for low spot number. Since hybrids of both sexes were sterile, no further investigations of this trait were performed.

Number of papillae on the anterior spiracles is also diagnostic for the two species, though the difference is not as great. The hybrid was significantly different from *O. longicornis* for all *O. longicornis* populations pooled. However it was not different from the Tucson population when compared alone. Dominance for this trait appears to be incomplete in the hybrids.

Odontoloxozus pachycticola Mangau and Baldwin, NEW SPECIES

Description. — *Head*: Brown, heavy grey pruinosity anterior to compound eye, remaining surface lightly dusted or bare. Genae lightly dusted, post-orbital surface heavily pruinose. Base of antennae shiny brown-black. Antennae porrect, brown, lightly pruinose.

Thorax: Scutum grey, pruinose with three median, longitudinal dark brown vittae. Center vitta extended to presutural area of scutellum, lateral vittae end just posterior to transverse suture. One row of dorsocentral bristles lateral to vittae, occasional bristles scattered longitudinally over median third of scutum. Lateral surfaces of scutum appearing slightly darker than medial dorsal surface due to a patch on each dorso-lateral surface and numerous dorso-central, supra-alar, and intra-alar bristles, each with a dark patch at base. Pleura and coxae grey, densely pruinose. Anepisternum with 17 to 25 spots (Table 1). Legs with trochanters, femora and tibiae yellow-brown to brown. Femora distally with two dark bands; tibia slightly darker at distal end; tarsi dark brown with black bristles. Wings identical to *O. longicornis*.

Abdomen: Terga laterally dark grey on median and posterior surfaces, pruinose on anterior surfaces. Male and female genitalia yellow, male surstylus with 4 gripping lobes at end of elongated epandrium. Aedeagus coiled inside epandrium. Female with elongate, retractable ovipositor tapering from bulbous base to narrow distal portion. Genitalia of both sexes not distinguishable from *O. longicornis*.

Holotype ♂ and 5 paratypes, 3 ♀ and 2 ♂, from El Centenario, Baja California, Mexico, 15 km west La Paz Baja California. Reared ex. *Lophocereus schottii*

Table 1. Morphological comparisons of *O. longicornis* and *O. pachycticola* and their hybrids.

Species	Character	Mean	SD	CV (%)	N
<i>O. pachy.</i>	anepistern. spots	20.82	3.12	14.9	28
<i>O. long.</i> (Maz.)	anepistern. spots	43.80	6.13	13.9	20
<i>O. long.</i> (Kino)	anepistern. spots	46.59	7.28	15.6	23
Hybrids	anepistern. spots	23.42	4.31	15.6	7
<i>O. pachy.</i>	spir. papillae	27.60	1.90	6.9	30
<i>O. long.</i> (Maz.)	spir. papillae	35.53	2.08	5.8	30
<i>O. long.</i> (Kino)	spir. papillae	32.81	2.45	7.4	16
Hybrids	spir. papillae	31.69	3.19	10.0	16

(Engelm.) April 1975. Deposited in National Museum of Natural History, Washington, D.C.

Etymology: The specific epithet *pachycticola* is derived from the subtribe Pachycterinae of the Cactaceae (see Gibson and Horak, 1978), the “thick stem” columnar cactus taxon in which the species commonly breeds.

Odontoloxozus longicornis and *O. pachycticola* are easily separated by differing numbers of bristles (with dark patches at their base) on the lateral thoracic areas of adults. Third stage larvae and puparia are separated by differing numbers of papillae on the anterior spiracles. Because both of these characters are readily quantifiable, they are used for identification of species and may be useful for detection of hybridization in natural communities. Neither of these characters changed in response to any of the environmental conditions including changes from cactus diet to artificial medium or to changes in temperature and humidity.

Chromosomal analysis.—Idiograms for the two species are given in Fig. 1 along with relevant percent of total chromosome length and centromeric indices for autosomes and X chromosomes. The species can easily be identified by differences in chromosome number and morphology. The karyotype of *O. longicornis* consists of 5 submetacentric autosome pairs; sex chromosomes are more heavily stained and the X chromosome is polymorphic. The Y chromosome has only been observed in testes material. It is about 50% the size of autosome 5 and darkly stained. Females in the Kino population are frequently heterokaryotypic. The karyotype of *O. pachycticola* has 6 autosome pairs, all are more submetacentric than in *O. longicornis* and 2 autosomes (V and VI) are smaller than any *O. longicornis* autosomes. We did not find any karyotypic polymorphism in 30 individuals of this species.

Polytene chromosomes of the two species and hybrids are shown in Figs. 2–4. Chromosomes of *O. longicornis* (Fig. 2) generally show extensive ectopic pairing and sometimes have a distinct chromocenter. Chromosome ends of this species are usually attached, making identification difficult. Polytenes of *O. pachycticola* (Fig. 3) normally do not show ectopic pairing, ends are free and arms can be easily recognized. For the hybrids (Fig. 4) chromosomes pair along regions of homology, but there is no synapsis. In hybrids, 1 chromosome (A) shows homeologous pairing for most or all of the length. In others (B) there is pairing but loops are present indicating deletions, translocations or other differences in the pair. Other chromosomes (C) show a complex of homologies suggesting a number of rearrange-

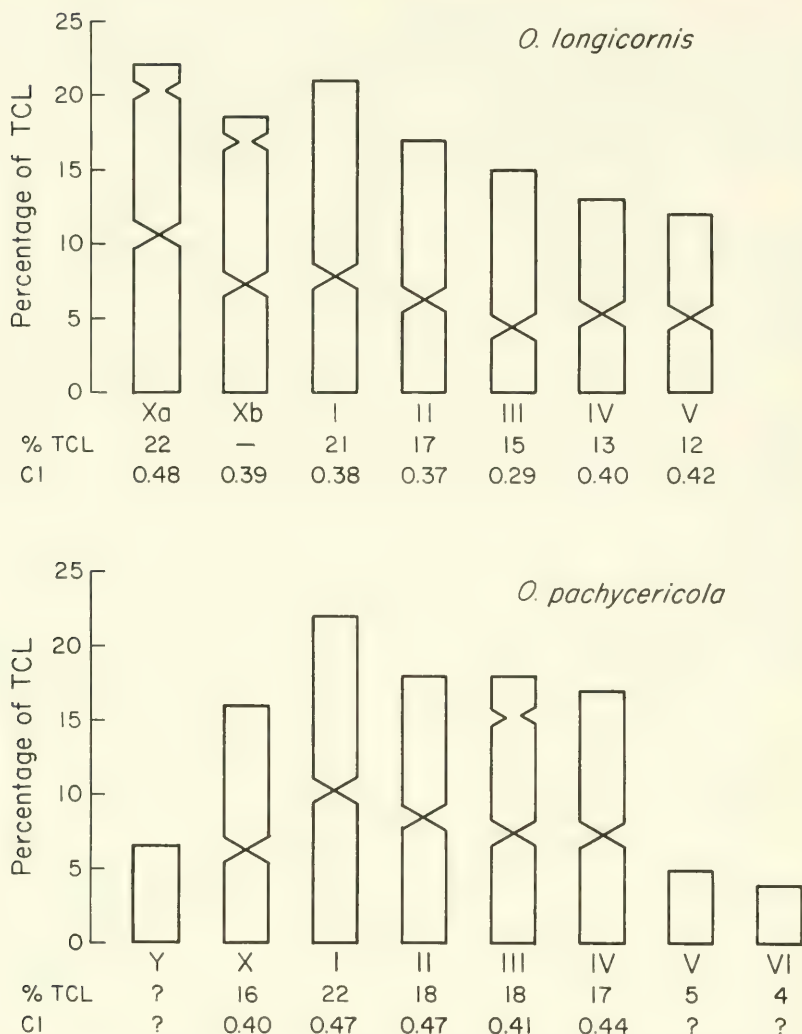


Fig. 1. Idiograms of the two *Odontoloxozus* species with relevant chromosome data. The Y chromosome in *O. longicornis* is similar in morphology to *O. pachyericola* but has not been measured in a complete karyotype.

ments and Robertsonian changes. Hybrids formed from crosses among the 3 populations of *O. longicornis* did not show any polymorphism in polytenes.

Mating time analysis. — Mating behaviors of *O. longicornis* and *O. pachyericola* were observed under field and laboratory conditions. Males mount females by jumping to a position above the female or by pulling the female under them with their forelegs, neither display or dancing behavior has been noted. Males use their hind legs to position the terminal abdominal segment of the female while standing over the female. Females may escape by running from the guarded position without copulating; males rarely follow to make further attempts (Mangan, 1979).

Variation in mating time, measured as the total period of genital contact, is summarized in Fig. 5 and analyzed in Table 2 for populations of *O. longicornis*

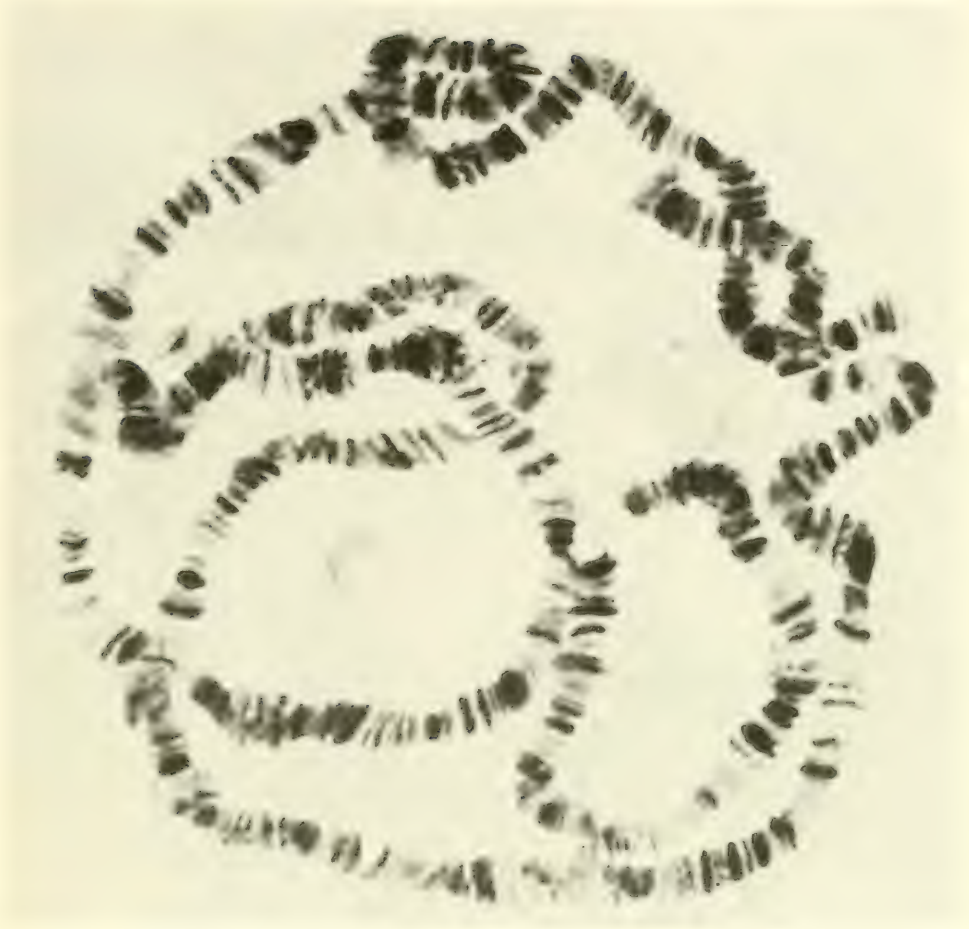


Fig. 2. Polytene chromosomes from salivary glands of *O. longicornis*.

in the Sonoran desert and *O. pachycericola* from the cape region of Baja California. These data show apparent differences in interpopulation crosses which affect mating times. Dissections of three females from matings interrupted after thirty seconds showed that sperm is transferred in this short time. Length of the copulatory period is apparently determined by the male. No differences in male genital morphology, which could cause difficulties in insertion or extraction of the aedeagus, were noted. All matings were terminated by the males extracting the aedeagus with little apparent effort.

Analysis of mating time data was performed using a series of simple analysis of variance models for each component (sex and population) and type of mating (intra- or inter-specific). There were a total of 133 tests. For each type of fly, classified by locality of source population and sex, all matings either involved that type or did not. The analysis model treated mating time as a dependent variable with fly type (sex and locality) as the independent variable. Since there were different numbers of matings for each type, the powers of these tests are not all exactly equal. They are generally comparable as to whether the type was



Fig. 3. Polytene chromosomes from salivary glands of *O. pachyericola*.

significant or not. Clearly crosses between mainland males (*O. longicornis*) and La Paz females (*O. pachyericola*) are the strongest contributors to variation in mating time in these analyses and in Fig. 2.

Species distributions.—Ryckman and Olsen reviewed in some detail distributions of *O. longicornis* in north and central America. They included in their survey specimens from '6 mi. E. La Paz' Baja California, this is in the region we sampled for *O. pachyericola* and probably represents this species. The distribution for *O. longicornis* includes the Sonoran and Mohave desert regions of California and Arizona. Steyskal (1965) gives morphological notes for larval specimens of *O. longicornis* collected in Harlingen, Texas (lower Rio Grande Valley). We have collected specimens of *O. longicornis* from regions around El Paso, Texas and the upper Rio Grande Valley (Starr County) in Texas. This apparently represents the eastern limit for this species in the U.S.

We attempted to discover possible zones of sympatry for these species by collecting or securing specimens from likely areas. We examined larval specimens from San Esteban and Tiburon islands in the Gulf of California, west of Bahia Kino, Sonora, these samples had means of 32.75 (SD = 1.38, $n = 8$) and 33 (SD =



Fig. 4. Polytene chromosomes from salivary glands of a hybrid formed from *O. pachycericola* and *O. longicornis*.

2.82, $n = 2$) total spiracular papillae respectively, indicating that these islands are occupied by *O. longicornis*. Larval illustrations of specimens from Los Angeles County, California by Olsen and Ryckman (1963) show the spiracles of their specimens to be within the range for the Sonoran desert samples of *O. longicornis*. Four adult specimens collected by W. T. Starmer from San Telmo, Baja Ca. Norte in 1979 had 36 (SD = 6.73) anepisternal spots, indicating that this region is occupied by *O. longicornis*. Based on this evidence then, we have not found any zones of sympatry for the two *Odontoloxozus* species. Furthermore, we suggest that for northern Mexico and the southern desert regions of the U.S.A. there are still only two known Neriidae, *O. longicornis* and *Onecopsis flavifrons* (Bigot).

Recently one of us (RLM) has collected and examined 23 specimens from columnar cacti (*Lemaireocereus* prob. *pruinosis*) in central Chiapas (6 km SE Tuxtla Gutierrez) averaging 35.48 (SD = 3.53) spots on the left anepisternum.

Table 2. Single factor analysis of variance (ANOVA) results for tests of effects of population, and types of mating on time in copula.

Factors		Statistics (ANOVA df = 1,131)	
Population	Sex	F value	P <
Tucson	M	3.221	.075
Tucson	F	9.196	.003
Mazatlan	M	.488	.486
Mazatlan	F	6.645	.011
Kino	M	.220	.640
Kino	F	3.315	.071
La Paz	M	1.022	.314
La Paz	F	58.515	<.001
Type Mating			
Allopatric*		36.861	<.001
Mating#		.832	.363

* La Paz $\times$ Non-La Paz (i.e. interspecific).

Sequence number of mating, e.g. 1 is first mating, 2 is second etc.

Available evidence thus indicates that samples from central Mexico and Central America listed in Ryckman and Olsen (1963) are correctly identified as *O. longicornis*.

DISCUSSION

From this analysis we view the most likely speciation process in *Odontoloxozus* as having been allopatric, there being no evidence of secondary contact. Lack of host plant specificity among populations in this and previous studies (Ryckman and Olsen, 1963) and the transient nature of the cactus substrates suggests that sympatric or stasipatric host plant associated factors were not likely to have been involved in this isolation. In other insect groups, host plant specificity or sedentary habits have been associated with behavioral and chromosomal processes leading to speciation (see White, 1978 for review). In the cape region of Baja California, isolated stands of senita cacti in river flood plains and hecho cacti at higher elevations may have served as substrates for small spatially isolated populations. In these populations chromosomal aberrations could become fixed (see Bush, 1975).

Morphological analysis of the hybrids of these species indicates varying degrees of dominance for certain quantitative characters. Anepisternal spot number for hybrids, pooled for crosses in both directions is slightly higher than, and statistically significant from, *O. pachycericola*. Anterior spiracular papilla number showed less dominance with a mean intermediate between that for *O. pachycericola* and *O. longicornis*. No obvious differences were noted in adult sizes in the species, therefore it is doubtful that nutritional differences are directly responsible for the difference in spiracular morphology. Coefficients of variation for all measurements indicate nearly twice the variation in mesopleural spot number than spiracular papilla number.

Hybrid matings, in addition to producing reproductively inviable offspring, incur extensive costs in terms of mating time investments. Mangan (1979) showed that for *O. longicornis*, male mating fitness can quite adequately be appraised as

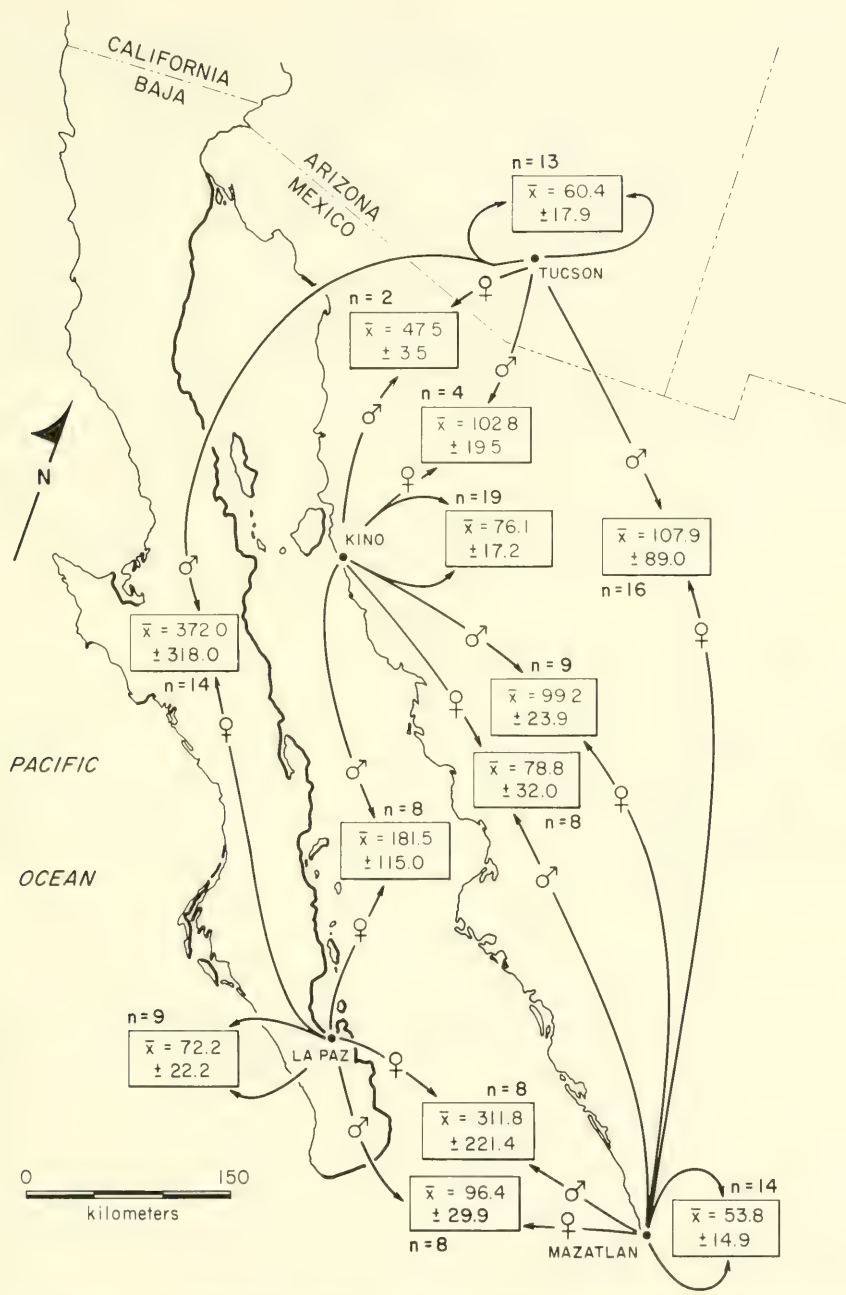


Fig. 5. Mating times (in seconds) from various crosses among Sonoran desert and Baja California populations.

an offspring gain per minute investment ratio. Extended mating time investments by *O. longicornis* males in hybrid matings incur an average of three to eight times the time investment for a normal mating with no gain. We hypothesize that *O. longicornis* males would be under heavy selection pressure to avoid such matings if regions exist where populations of the two species are sympatric. While such selection has been a part of classical speciation theory (Mayr, 1942) this process is not accepted as a part of speciation by all systematists (Futuyma and Mayer, 1980; Paterson, 1978, 1981).

Repeated matings by both gravid and immature females were noted by Mangan (1979) for *O. longicornis*. According to theoretical treatments by Parker (1974) and experimental studies by Prout and Bundgaard (1977) with *Drosophila*, genetically controlled fitness differences in terms of sperm competition in species with multiple mating are significant components of overall reproductive fitness. The lengthening of mating times between individuals from different species or populations separated by long distances (Tucson-Mazatlan) may reflect differences in adaptation of male behavior or physiology to local female reproductive systems. Behavioral and genetic divergence of Tucson and Mazatlan populations suggests the possibility of clinal evolution over the range of *O. longicornis*.

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NEW RECORDS OF PHYCITINAE FROM MEXICO AND A
DESCRIPTION OF A NEW GENUS AND SPECIES
(LEPIDOPTERA: PYRALIDAE)¹

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Abstract. The following species are recorded from Mexico for the first time: *Difundella corynophora* Dyar; *Atheloca subrufella* (Hulst); *Caristanius decoloralis* (Walker); *Stylopalpia scobiella* (Grote); *Comotia torsicornis* Dyar; *Unadilla maturella* (Zeller); *Baphala homoeosomella* (Zeller); *Entmemacornis proselytes* Dyar. *Nefundella*, new genus, is established for three species: *N. distractor* (Heinrich) (type-species), new combination; *N. tolerata* (Heinrich), new combination; and *N. xalapensis*, new species, from SE of Xalapa, Vera Cruz, Mexico.

Heinrich (1956) included information on the species of Phycitinae then known to occur in Mexico. Since that time little has been added to our knowledge of the Mexican phycitine fauna. McGuffin (1967), and Hedlin et al. (1981), contributed information on Mexican *Dioryctria*, and a new species of *Acrobasis* was recently described from Mexico (Neunzig, 1983).

In this paper, based on adult phycitines collected recently in eastern Mexico, I list species previously not recorded from Mexico and describe a new genus and species. Except as noted, the specimens are deposited in the North Carolina State University Insect Collection (NCSU).

NEW RECORDS FOR EASTERN MEXICO

Difundella corynophora Dyar: One male of this distinctive species was collected on 25 July, 1984, 4 km south of Estacion Palenque, Chiapas. Previously recorded by Heinrich (1956) from Cayuga and Chejel, Guatemala; La Chorrera, Panama; and Cayenne, French Guiana.

Atheloca subrufella (Hulst): One male of this species was collected on 1 August, 1984, 5 km west of Pisté, Yucatan. Previous distribution records include Florida (throughout state); Pinal del Río, Cuba; and Kingshill, Virgin Islands (Heinrich, 1956). Kimball (1965) listed cabbage palm (*Sabal palmetto*) (Walter) Lodd ex. Schultes), and saw palmetto (*Serenoa repens* (Bartram) Small) as the larval food plants of *A. subrufella* in Florida. Various members of the palm family (Arecaceae) are probably utilized by *A. subrufella* as larval hosts in the Neotropics.

Caristanius decoloralis (Walker): Five males and two females of this species

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were collected 5 km south of Vera Cruz, Vera Cruz, on 22 July, 1984. Heinrich (1956) listed only the southeastern United States as the range of this species, but did include Brownsville, Texas, adjacent to the Mexican border. Larvae of *C. decoloralis* feed on several species of *Cassia* (Fabaceae) in the southeastern United States (Neunzig, 1979), and most likely *Cassia* is also the host in Mexico.

Stylopalpia scobiella (Grote): *Stylopalpia scobiella* was found to be a relatively abundant species at a site located 5 km south of Vera Cruz, Vera Cruz. Eight males and five females were collected on 22 July, 1984. Previous distribution records for this species include several localities in Texas, and Glenwood Springs, Colorado (Heinrich, 1956). Heinrich's speculation that *S. scobiella* also occurred in Mexico proved to be correct.

Comotia torsicornis Dyar. (Fig. 7): Five males and four females were collected on 1 August, 1984, near Pisté, Yucatan. Heinrich (1956) based his treatment of this species solely on the male type, because no females were available from the type-locality or elsewhere that appeared to be conspecific. Because the female of *C. torsicornis* apparently has not been described, I illustrated the genitalia of one of the four females collected near Pisté. *C. torsicornis* has previously only been reported from Porto Bello, Panama (Heinrich, 1956).

Unadilla maturella (Zeller): Two males and one female of this species were collected 21 July, 1984, at Ciudad Valles, San Luis Potosi. Previous collections were from Colombia; Cayuga, Guatemala; and Baracoa and Havana, Cuba (Heinrich, 1956) and Dominica (Shaffer, 1978).

Baphala homoeosomella (Zeller): Two males and two females were collected 25 July, 1984, 4 km south of Estacion Palenque, Chiapas. According to Heinrich (1956), this species is apparently common, and widely distributed in tropical America. Previous records include Cuba; St. Croix, Virgin Islands; Barro Colorado Island, Para Iso, Tobago Island, and Rio Trinidad, Panama; Georgetown, Guyana; Honda, Columbia; and São Paulo, Brazil. The larvae of *B. homoeosomella* are predaceous on scale insects.

Entmemacornis proselytes Dyar: One male of this species was collected 15 km southeast of Xalapa, Vera Cruz, on 23 July, 1984. The only other specimens of this species reported in the literature belong to the type-series (2 males, 2 females; Cayuga, Guatemala).

***Nefundella* Neunzig, NEW GENUS**

Type-species: Difundella distractor Heinrich, 1956.

Heinrich (1956) included four species in his treatment of *Difundella* Dyar. He was aware, however, that these species did not form a closely knit unit, and he tentatively divided the species into two distinct morphological groups of two species each. A new species recently collected in Mexico provided additional support for a more formal separation of these groups.

In the genus *Difundella* are retained the two species *corynophora* Dyar and *subsutella* (Schaus), which share the following morphological features: labial palpus reaching above vertex; hindwing with cell less than one-third length of wing; vein 2A of hindwing of male bent before middle and with a tuft of yellow, setae-like scales on its underside (within bend); gnathos greatly reduced, its apical projection fine, needle-like; costa of valva simple. To *Nefundella* are assigned *distractor* Heinrich, 1956, *tolerata* Heinrich, 1956, and the new species described



Fig. 1. *Nefundella xalapensis*, holotype.

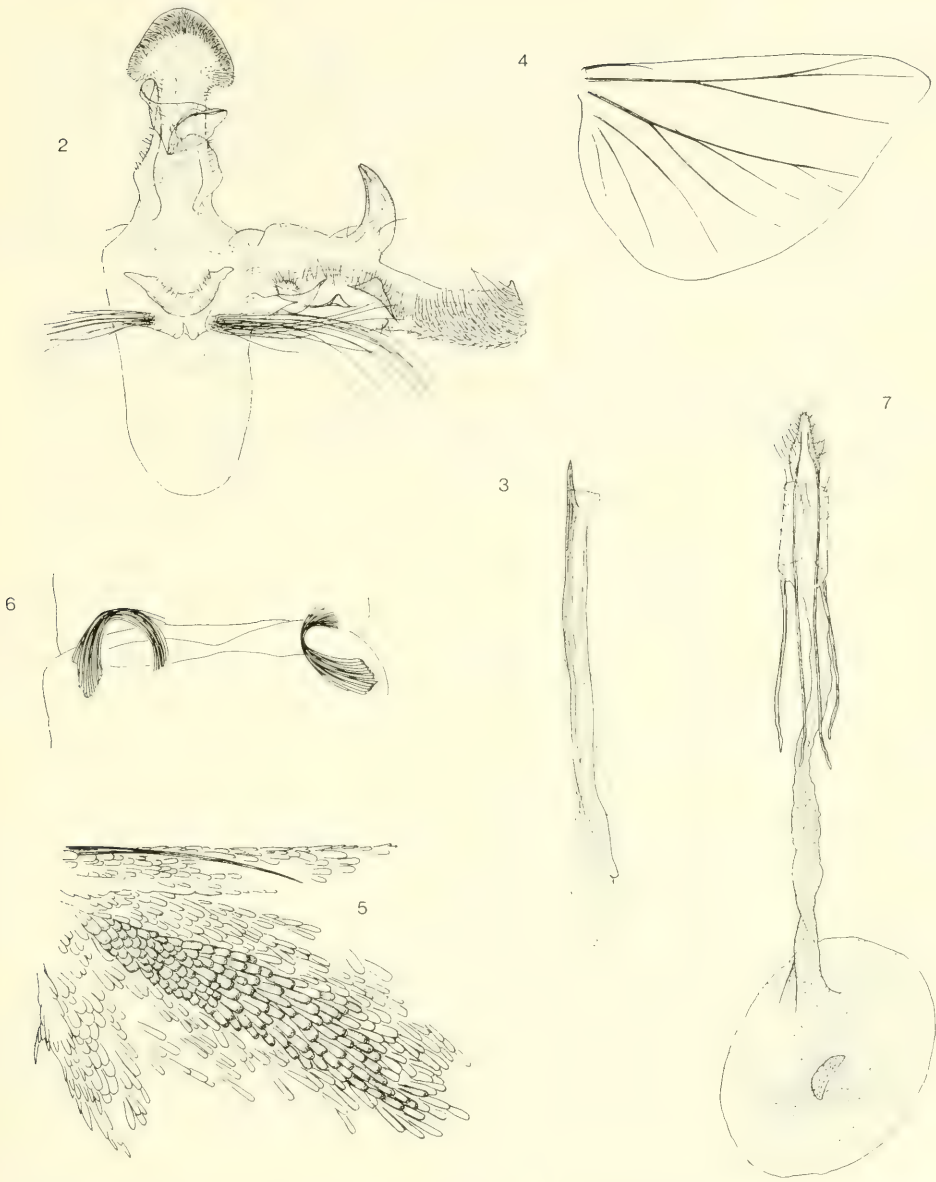
below. Diagnostic features of *Nefundella* include: labial palpus not reaching vertex or barely reaching vertex; hindwing with cell more than one-third (but less than half) the length of wings; vein 2A of hindwing of male not bent, without setae-like scales on its underside, but instead with a patch of decurved androconia (sex-scales) along base of Cu on underside; gnathos with apical process enlarged and strongly sclerotized; costa of valva with strongly sclerotized projection(s).

Difundella and *Nefundella* are both New World, neotropical elements. Nothing is known of the larval hosts of any of the included species.

Nefundella xalapensis Neunzig, NEW SPECIES

Figs. 1–6

Description.—*Head*: Pale golden-brown with some reddish-brown on vertex. Labial palpus barely reaching vertex, pale golden-brown. Maxillary palpus squamous, pale golden-brown. Basal segment of antenna simple, pale golden-brown to reddish-brown, shaft filiform, with abundant, very short sensilla trichodea (cilia). *Collar*: Pale golden-brown dorsally, pale golden-brown ventrally with distinct row or patch of black scales. *Forewing*: Brown above, dusted with white, white most prevalent in basal and subbasal areas; a few scattered black scales in basal and subbasal areas, and to a lesser extent over rest of wing; antemedial line very weakly developed, pale golden-brown, without black border; discal spot pale golden-brown; postmedial line very pale golden-yellow, preceded by row of contrasting black scales. Terminal margin with row of black scales. Length of forewing 6.0–7.0 mm. *Hindwing*: Pale brown above, brown along margins. Undersurface with patch of golden scales (Fig. 5), distal margin of each scale forming patch curled toward wing. *Abdomen*: Lateral pockets and curved scale tufts (Fig. 6) between segments 2 and 3. *Genitalia* (Figs. 2, 3): Uncus broadly sagittate; apical process of gnathos greatly enlarged, sclerotized; sacculus of valva with a relatively short, nearly triangular process; costa of valva with large, bifurcate, spine at about



Figs. 2-6. *Nefundella xalapensis*. 2, Male genitalia, left valva and aedeagus removed. 3, Aedeagus. 4, Right hindwing. 5, Undersurface of base of left hindwing. 6, Ventral scale tufts between abdominal segments 2 and 3. Fig. 7, *Comotia torsicornis*, female genitalia, ventral aspect.

mid-costa, and very small conical spine at apex; anellus robust, shallowly V-shaped; aedeagus long, slender, tapering to a point; vinculum slightly longer than its greatest width.

Type material.—*Holotype*: ♂; Mexico: Vera Cruz, 15 km SE of Xalapa, 23-VII-84, H. H. and K. M. Neunzig; ♂ genitalia slide HHN 979: in NMNH. *Paratype*: One ♂; same collection data.

Distribution.—Known only from type-locality.

Discussion.—*N. xalapensis* appears to be most closely related to *N. distractor*, but lacks the distinct black scaling outlining the antemedial line of *distractor*. There are also several differences in the male genitalia: the uncus is spoon-shaped in *distractor* and sagittate in *xalapensis*; the anellus is u-shaped in *distractor* and v-shaped in *xalapensis*; the sacculus bears a large, curved subtriangular element in *distractor* and a much smaller, nearly triangular element in *xalapensis*; the apex of the valva is enlarged and rounded in *distractor* and more evenly produced with a small, conical spine in *xalapensis*.

KEY TO SPECIES OF *NEFUNDELLA*

1. Uncus slightly broadened and rounded toward apex; valva with a small, thornlike process near mid-costa *N. tolerata* (Heinrich)
- Uncus spoon-shaped or sagittate; valva with a large, hooked process near mid-costa 2
2. Valva with apex distinctly enlarged, rounded, unarmed *N. distractor* (Heinrich)
- Valva with apex only slightly enlarged, with a conical spine *N. xalapensis* n. sp.

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I thank J. K. Liebherr of Cornell University for the loan of the slide of the genitalia of the holotype of *Difundella distractor* Heinrich. Also, Kurt M. Neunzig provided valuable assistance in the collection of most of the included species.

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A NEW NEARCTIC SPECIES OF *CONTARINIA*
(DIPTERA: CECIDOMYIIDAE) RECENTLY INTRODUCED
INTO HAWAII ON *CUPRESSUS* (CUPRESSACEAE)

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Abstract.—*Contarinia rugosa*, n. sp., is described from specimens taken from buds of Arizona cypress in Hawaii. The new species was introduced into Hawaii on infested plants from California. The new taxon forces a redefinition of *Contarinia* to include species with short ovipositors.

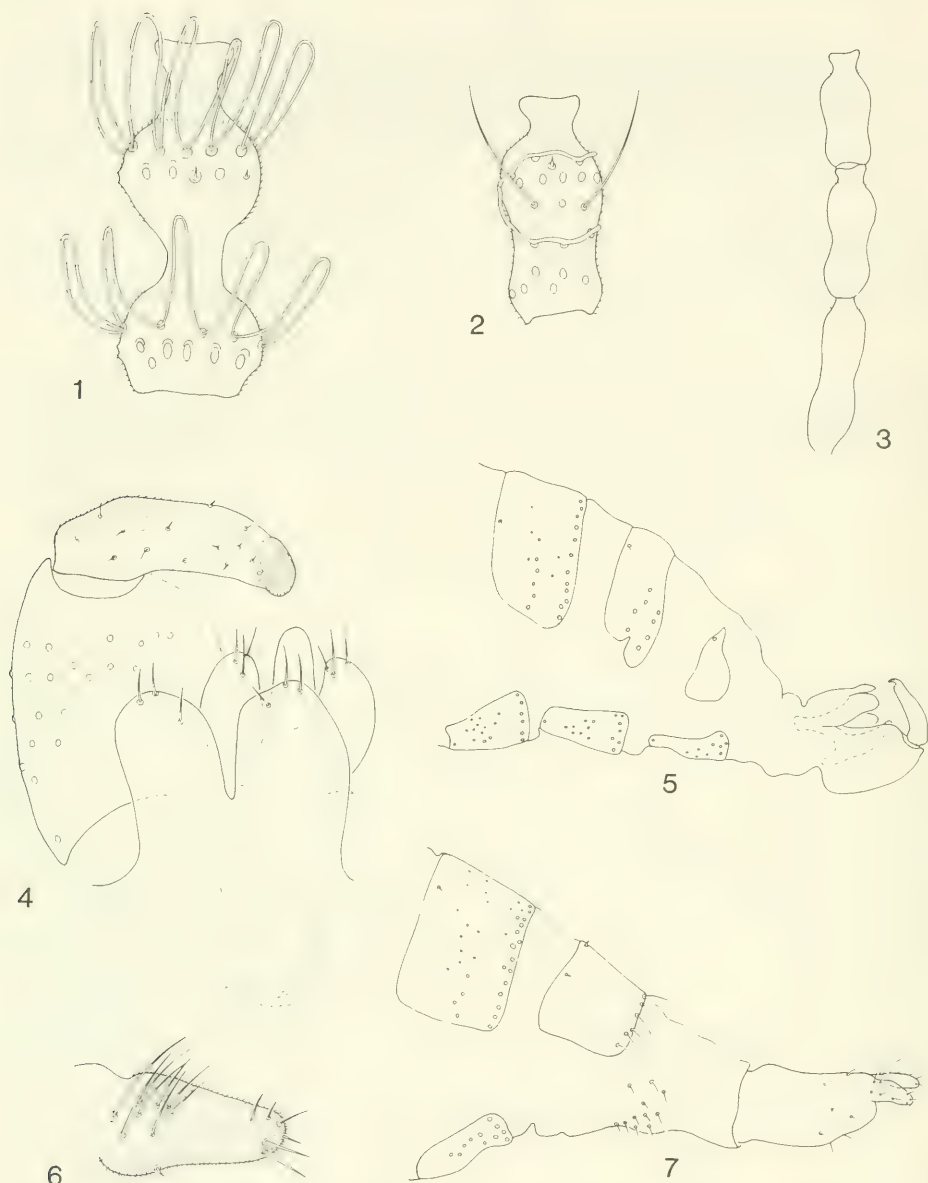
This new species was discovered in June, 1984 in a large infestation of buds of Arizona cypress in a nursery in Maui, Hawaii. The new buds had turned brown and died. Personnel of the Hawaii State Department of Agriculture subsequently collected adults and larvae of the new species from the host plants, *Cupressus arizonica* Greene (Cupressaceae). *Cupressus* is not native to Hawaii but has been imported extensively for ornamental use. The infested plants were received from a nursery supplier in California. Further evidence that this new species is from North America is the presence of a short series in the National Museum of Natural History, Washington, D.C., of a similar if not the same species that was reared from buds of another cypress in California. The damage to cypress in Hawaii is similar to that on *Juniperus* spp. made by *Oligotrophus betheli* Felt, a widespread North American cecidomyiid. Larvae of both species live singly in apical buds. The buds do not elongate and the larvae remain covered by the apparently unmodified bud scales. The branch tips turn brown and die when the larvae cease feeding. The larva pupates in the bud and adults emerge a short time later. Both species are multivoltine.

Contarinia is a very large genus, currently with about 275 described species. I know of about 45 undescribed species from North America. The genus serves as a paraphyletic omnibus category for species that do not fit in any other related genus. The short ovipositor and rugose larval integument make this new species unique in *Contarinia*.

Contarinia rugosa Gagné, NEW SPECIES

Figs. 1-9

Adult.—*Head*: Eyes large, about 7 facets long at vertex, facets circular, contiguous except near midheight of eye where they are up to $\frac{1}{3}$ facet diameter apart. Occiput rounded, without peak. Frontoclypeal setae 3-4 per side. Labella hemispherical in frontal view, each with 3-4 setae. Palpus 4-segmented. Male antennal flagellomeres binodal, bicircumfilar, the circumfilar loops attaining the next distal



Figs. 1-7. *Contarinia rugosa*. 1, Male third flagellomere. 2, Female third flagellomere. 3, Female first through third flagellomeres. 4, Male terminalia (dorsal). 5, Male abdominal segments 6 to end (lateral). 6, Female abdominal segments 7 to end (dorsolateral). 7, Female cercus (dorsolateral).

node (Fig. 1). Female antennal flagellomeres 1-3 as in Fig. 3; circumfilar loops appressed (Fig. 2).

Thorax: Scutum with sparse setae placed mostly in a single row that is interspersed with few scales. Mesanepisternum with few scattered scales on dorsal half. Mesepimeron with 7-10 setae. Wing length: male, 1.7-2.0 mm (1.8, avg. of 4);



Figs. 8–10. *Contarinia rugosa*. 8, Larval spatula and adjoining papillae. 9, Larval terminal segments (dorsal). 10, *Contarinia* sp., larval spatula.

female, 1.7–2.3 (2.0, avg. of 6). Rs slightly bowed apically, joining C behind wing apex; C broken at juncture with Rs. Claws slightly shorter than empodia.

Male abdomen (Figs. 4–5): Tergites 1–6 rectangular with basal pair of trichoid sensilla, a single uninterrupted caudal row of setae, 4–10 lateral setae, and sparse, scattered scales; tergite 7 weakly sclerotized mesocaudally, with basal pair of trichoid sensilla, 3–5 caudal setae laterally, 4–5 lateral setae in separate group, and 0 to 2 scales laterally; tergite 8 sclerotized only laterally, usually bare except for basal pair of trichoid sensilla. Sternites 2–6 rectangular, with pair of closely approximated, basal trichoid sensilla, a mostly single, caudal row of setae, and with mixed setae and setiform scales grouped near midlength; sternites 7 and 8 as for preceding except with 2 caudal rows of setae. Terminalia (Fig. 4): cerci broadly rounded; hypoproct deeply divided, its lobes broad, rounded at apex, with several setae apically and ventrally; aedeagus broad, rounded at apex, slightly longer than hypoproct; gonopod stout, apodeme rounded anteriorly; gonostylus narrowing slightly from base to apex, mostly striate, setulae present basolaterally and basoventrally, evenly setose throughout.

Female abdomen (Figs. 6–7): Tergites 1–7 and sternites 2–7 generally as for male but tergal scales and caudal setae more numerous. Tergite 7 about .56 length of distal half of ovipositor. Tergite 8 about as long as 7, with pair of trichoid sensilla and single, sparse, caudal row of short setae. Ovipositor short, barely protrusible, proximal half anteriorly with scattered lateral and ventral setae, distal half posteriorly with scattered short setae, completely setulose, unstriated; cerci broad, rounded at apex, completely setulose, setae concentrated at base and apex.

Larva (last instar).—Length, ca. 2 mm. Integument rugose. Anterior margin of spatula divided into 2 rounded projections (Fig. 8). Full complement of papillae typical of *Contarinia* present including corniform pair of terminal setae (Fig. 9); all setae very short and difficult to see because of general rugosity of integument.

Holotype.—♂, ex *Cupressus arizonica*, Olinda, Maui, Hawaii, 2600', 6 June, 1984, M. Miyahira. Paratypes: 2 ♂, 5 ♀, same data; ♀, same locality, 10 July, 1984; ♂, ♀, and 5 larvae, same locality, 19 August, 1984; larvae, same locality, January, 1985.

This species is similar to a series of poor specimens from buds of *Cupressus macrocarpa* Hartw. collected in 1947 at Stinson Beach, California. The adults of that series might well be included with *rugosa*, but they are poorly mounted and

their parts are difficult to see. The one larva of that series has the same rugose integument and reduced papillar setae as *rugosa* but the spatula (Fig. 10) is somewhat different. I have not seen such great variation in any *Contarinia* species, so am inclined to believe that the California series represents a distinct species.

The definition of *Contarinia* is broadened to include species with a very short ovipositor. Ovipositors of *Contarinia* are typically long-attenuate with the cerci greatly narrowed and pointed, all modifications for depositing eggs in plant buds (Gagné, 1973, 1981). The short ovipositor is a primitive character state, and there is no evidence that the long ovipositor of the other *contarinias* evolved only once. E.g. *Contarinia sorghicola* (Coquillett) and *Contarinia catalpae* (Comstock), both species with long ovipositors, are not necessarily more closely related to one another than they are to *rugosa*. Other character states of *rugosa* besides the short ovipositor that I consider primitive in *Contarinia* are the setulose and broad female cerci, the broader lobes of the male hypoproct, and the broader aedeagus (the last two presumably correlated with the shorter and therefore broader ovipositor). Derived character states of *rugosa*, not necessarily synapomorphic with the same states found in other *contarinias*, are: bifilar male flagellomeres; lack of a postvertical peak; rounded eye facets; relatively few setae of the frontoclypeus and thorax; empodia slightly longer than claws; and the mostly bare gonostylus.

ACKNOWLEDGMENTS

I thank B. Kumashiro, P. Conant, and M. Miyahira of the Hawaii State Department of Agriculture, and G. Paulson of the Maui Cooperative Extension Service for the information they provided regarding this species and for the collections they made; K. M. Harris, Commonwealth Institute of Entomology, London, R. V. Peterson, Systematic Entomology laboratory, Washington, D.C., and K. Valley, Pennsylvania Department of Agriculture, Harrisburg, for reviewing the manuscript; and L. H. Lawrence, Systematic Entomology Laboratory, for inking the drawings.

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**A NEW SPECIES OF *CARDIOCHILES*
(HYMENOPTERA: BRACONIDAE) INTRODUCED INTO
FLORIDA TO CONTROL *DIAPHANIA* SPP.
(LEPIDOPTERA: PYRALIDAE)**

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Abstract. — A new species of the genus *Cardiochiles* is described from Colombia, Venezuela, and Trinidad. This parasitoid braconid attacks larvae of *Diaphania* spp. and is being colonized in Florida for future release against *D. nitidalis* and *D. hyalinata*.

Species of *Cardiochiles* are parasitoids of Lepidoptera larvae. They have been studied taxonomically for North America (Mao, 1945, 1949) but the species of South and Central America are unstudied. This new species is described in order to facilitate its identification and to provide a name in support of biological control studies in Florida.

This species of *Cardiochiles* was collected in Colombia and introduced into Florida by J. E. Pena and V. Wadill, University of Florida, in a biological control program against *Diaphania nitidalis* (Stall), the melonworm, and *D. hyalinata* (L.), the pickleworm. The parasitoid is being colonized in Homestead, Florida for future releases. In addition, the National Collection of Insects contains specimens from Venezuela reared from *D. hyalinata* and specimens from Trinidad.

***Cardiochiles diaphaniae* Marsh, NEW SPECIES**

Figs. 1-3

Female.—Length of body, 4.5–5.5 mm; ovipositor, 0.8–1.0 mm. Color: head, thorax and abdomen honey yellow; antennal pedicle and flagellum black, scape with brown stripe laterally, ocellar triangle black, vertex occasionally black between eyes across ocelli; apex of middle tibia and middle tarsal segments black, hind coxa with black spot dorsally at apex, hind trochanter black, apex of hind femur black; base and apex of hind tibia black, apex of hind tarsomeres black, occasionally last 4 tarsomeres black; median black spot on apical segments of abdomen, ovipositor sheaths black; fore wings hyaline, infuscated at apex beyond second cubital cell (Fig. 1), mediellen cell of hind wing infuscated at base. Head: smooth, face elongate (Fig. 2), malar space $\frac{1}{3}$ eye height, lower clypeal margin bidentate medially (Fig. 3), occiput deeply excavated so that vertex narrow at ocelli, eyes hairy, antenna 32–35 segmented. Thorax: mesonotum smooth, notauli deep and scrobiculate, mesopleuron smooth, propodeal carina very strong, central areola diamond-shaped. Abdomen: terga smooth, central diverging grooves on

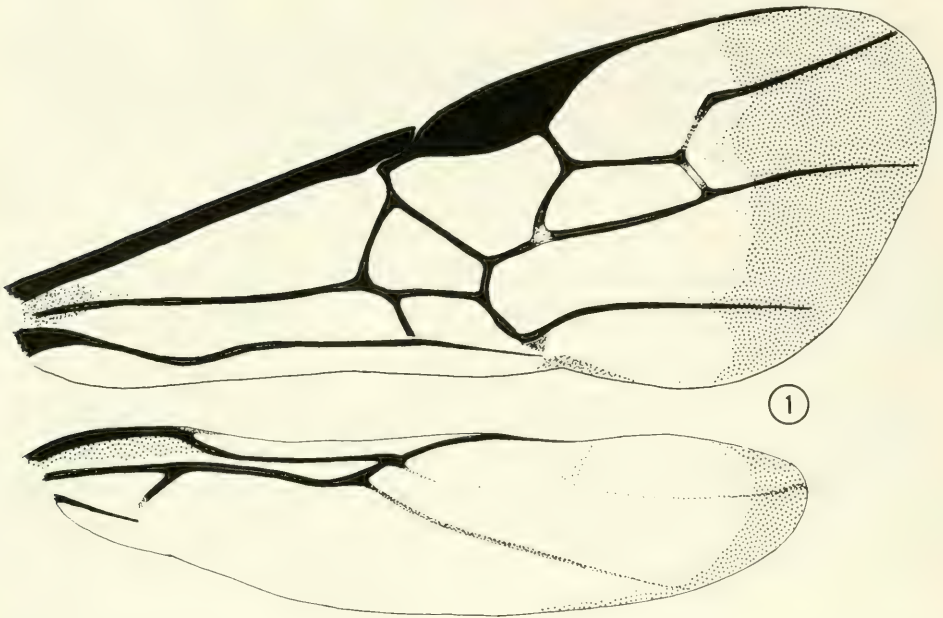


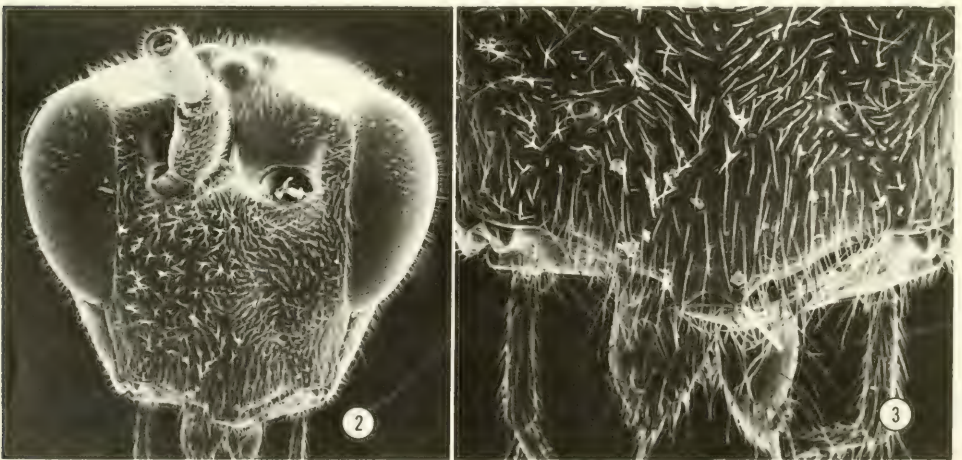
Fig. 1. *Cardiochiles diaphaniae* wings.

first tergum smooth, ovipositor about equal in length to $\frac{1}{2}$ hind basitarsus, sheaths broad and hairy. Legs: hind femur about 3 times as long as wide. Wings (Fig. 1): apical segment of radius sharply angled at base, first discoidal cell and median cell along medius nearly free of hair.

Male.—Identical to female except for usual sexual differences.

Holotype ♀.—Palmira, Colombia, VI-20-84, B. Gutierrez, reared from *Diaphania* sp. Deposited in National Museum of Natural History, Washington, D.C.

Paratypes.—2 ♀♀, 1 ♂, same data as holotype; 1 ♀, 1 ♂, Palmira, Colombia, I IV-



Figs. 2-3. *Cardiochiles diaphaniae*. 2, Face. 3, Clypeus.

16-84, J. E. Pena; 3 ♀♀, 1 ♂, Palmira, Colombia, VI-3-83 and VI-24-83, B. Gutierrez, Parasite of *Diaphania hyalinata*; 4 ♂♂, Palmira, Colombia, VIII-5-83, L. Quintero, ex. *Diaphania hyalinata*; 2 ♀♀, 3 ♂♂, Aragua, El Limon, Venezuela, VIII-9-68 and VIII-29-68, J. C. Marin-D. Villasmil-J. B. Teran, ex. larva of *Diaphania hyalinata*; 1♀, Maracay, Venezuela, VII-23-55, P. Guagliumi, parasite of *Diaphania hyalinata*; 1 ♀, 1 ♂, Caiman, Trinidad, III-17-61, N. Gopaul; 4 ♀♀, Aranguez Est., Trinidad, II-19-61, N. Gopaul; 1 ♀, St. Augustine, Trinidad, II-8-61; 6 ♀♀, 1 ♂, Curepe, Trinidad, III-27-61, N. Gopaul, VIII-7 to 12-77, malaise trap. Deposited in USNM, Canadian National Collection, and Florida Collection of Arthropods.

This species will run to *Cardiochiles ornatus* (Cresson) in Mao's (1945) key to the Mexican species. It is similar in overall coloration to *C. ornatus* from Mexico and *C. atricornis* (Ashmead) from the West Indies but both have completely infuscated wings rather than the apical infuscation on the wings of *diaphaniae*. In Mao's key to North American species (1949) *diaphaniae* will run to *C. theberiae* Rohwer but the body color (honey yellow) and wing pattern (hyaline with infuscated apex) will distinguish *diaphaniae* from all described North American species.

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FOUR NEW MOTHS FROM TEXAS
(LEPIDOPTERA, GEOMETRIDAE, NOCTUIDAE)

ANDRÉ BLANCHARD AND EDWARD C. KNUDSON

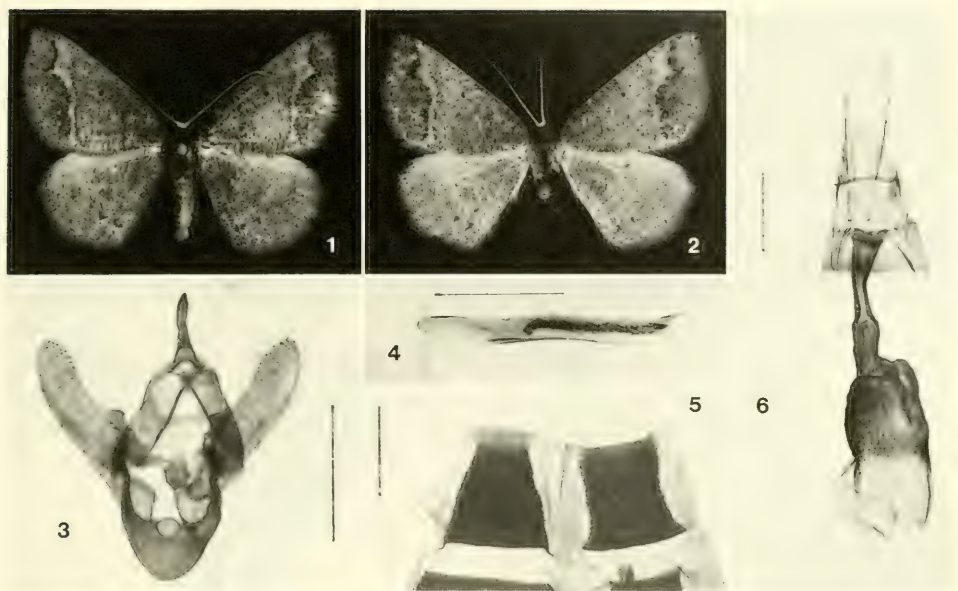
(AB) 3023 Underwood, Houston, Texas 77025; (ECK) 808 Woodstock, Bellaire, Texas 77401.

Abstract.—Four new species of Lepidoptera are described and illustrated from examples collected in Texas. In the Geometridae, *Drepanulatrix garneri* is described; in the Noctuidae, *Paramiana exculta*, *Euamiana adusta*, and *Tarachidia septuosa* are described.

Four new species are described from examples collected in UV light traps by the authors at various localities in Texas. The geometrid genus *Drepanulatrix* was revised by Rindge (1949), at which time only *D. bifilata* (Hulst) was known from Texas. Since that time, three additional species have been collected in Texas by us, including *D. unicalcaria* (Guenée), *D. hultsii* (Dyar), and the new species described below. In the noctuid subfamily Acontiinae, the closely related genera *Tarachidia* and *Acontia* are represented in Texas by more than 40 named species, as well as several that are apparently undescribed. These and other related genera are badly in need of revision, both at generic and specific levels. The taxon described below, however, is quite distinct from other North American species and is placed in *Tarachidia* with some reservations, though it agrees with the characters outlined for *Acontia* by Forbes (1954). In the amphipyridine tribe Noctoini, the genera *Euamiana* and *Paramiana* are extremely close, being chiefly distinguished by the presence or absence of a tubercle on the front (Robert W. Poole, pers. comm.). The two species described below were placed generically according to this character and also on the advice of Poole.

Drepanulatrix garneri, Blanchard & Knudson, NEW SPECIES

Male.—*Head*: Front dark reddish brown; vertex pinkish-ochreous between antennae, dark reddish brown behind. Labial palpi dark reddish brown, third segment slightly paler. Antennae bipectinate, except for terminal 13 segments, which are slightly serrate; scape and shaft of flagellum pinkish-ochreous dorsally, pectinations scaled dorsally, black with whitish at the extreme tip; beneath, unscaled, moderately setose. Thorax reddish brown, speckled with fuscous above; beneath light reddish brown, legs ochreous brown, hind tibiae speckled with black. Abdomen reddish brown above, paler beneath. *Forewings*: Ground color varies from pinkish-gray to orange brown, diffusely speckled with black, giving a purplish cast to the naked eye. Antemedial line weakly defined, blackish, nearly vertical from dorsal margin at $\frac{1}{3}$ the distance from base, slightly outwardly angled over cell, not clearly reaching costal margin. Postmedial line blackish, from dorsal margin



Figs. 1–6. *Drepanulatrix garneri*. 1, Holotype male. 2, Paratype female. 3, Male genitalia, aedeagus removed. 4, Aedeagus. 5, Eighth abdominal segment. 6, Female genitalia. Segment = 1 mm.

at $\frac{3}{4}$ the distance from base, nearly straight, not reaching costal margin. Subterminal line and the space between it and postmedial line constitute the most conspicuous feature of the maculation. The intervening space is not irrorated with black scales, as is the rest of the wing and thus appears much paler. Subterminal line complete or interrupted, black, from dorsal margin very near postmedial line and paralleling it to M_2 from where it diverges, forming an outwardly directed cusp just below M_1 , thence outwardly concave to costal margin. Subterminal space beyond subterminal line slightly more heavily irrorated with blackish. Discal spot black, well defined. Fringe concolorous with ground. *Hindwing* nearly concolorous with forewing, slightly paler towards cubital margin. Subterminal line defined only as 3 or 4 whitish margined black spots near anal margin. Discal spot inconspicuous above, but well defined on underside; fringe concolorous with ground.

Female.—As for male, except for simple antennae, paler ground color and reduced forewing pattern. *Length of forewing*: Males: $n = 3$, 15.2–16.8 mm, average 15.8 mm; female: $n = 1$, 16.1 mm. *Male genitalia* (Figs. 3–5): Uncus finely setose, mucronate at apex; gnathos obsolete; valves with rounded process at base of costa; juxta a shield-like plate; aedeagus elongate, with apical spur and a row of numerous, thorn-like cornuti, which extends slightly more than half the total length of aedeagus. Eighth abdominal segment represented in Fig. 5, sternite on the right. *Genitalia* (Fig. 6): Papillae anales membranous, moderately setose; apophyses thin, slightly hooked at apices; ostium bursae a well sclerotized, shallow cup; posterior $\frac{2}{3}$ of ductus bursae well sclerotized, dorso-ventrally compressed, anterior $\frac{1}{3}$ somewhat expanded and ridged; corpus bursae an elongate ovoid, posterior half sclerotized and encircled by a band of thorn-like scobinations near middle, anterior half membranous; ductus seminalis from posterior end of bursa.

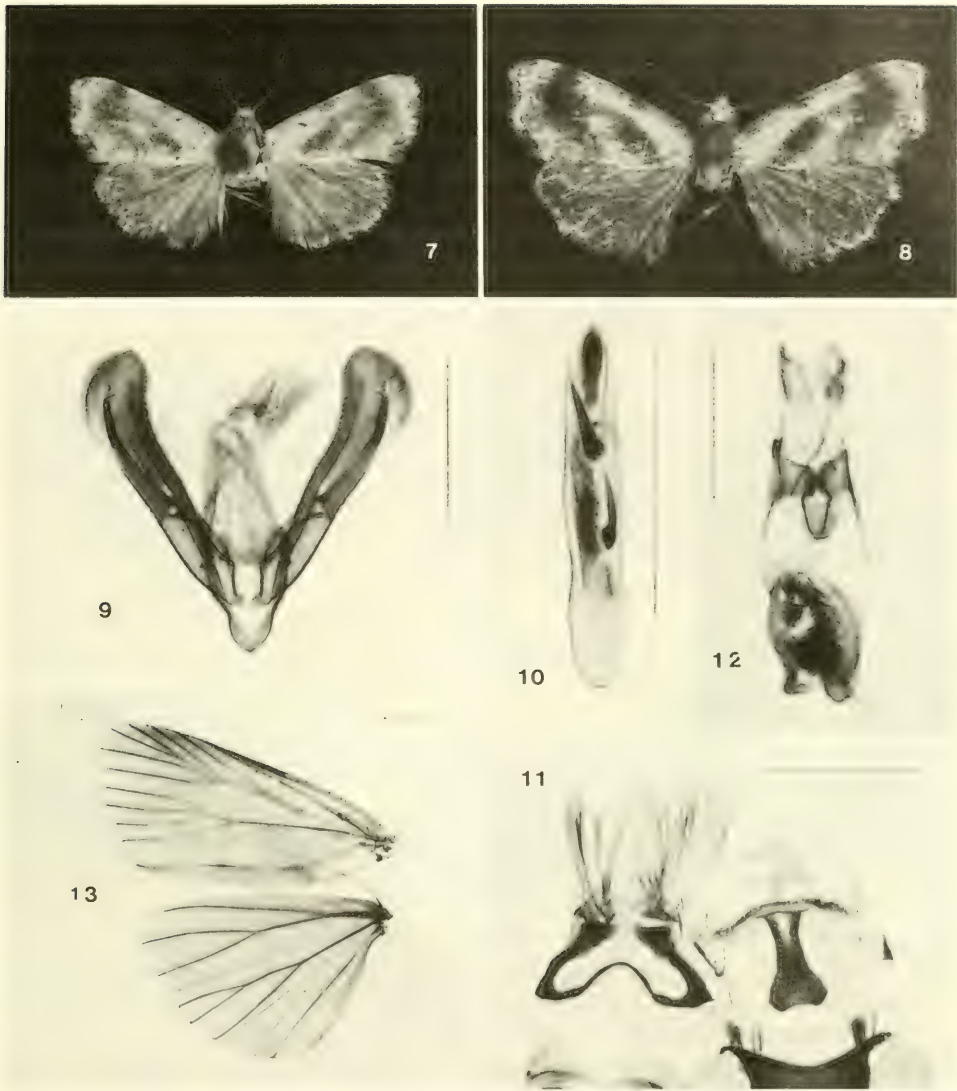
Types.—*Holotype*, ♂ (Fig. 1): Texas, Uvalde Co., Garner State Park, 24-III-85, collected by E. Knudson and deposited in the National Museum of Natural History. *Paratypes*: Same data as holotype, 1 ♂ (genitalia on slide ECK 1121 and represented in Fig. 5), 1 ♀ (genitalia on slide ECK 1123, represented in Figs. 2, 6 and deposited in the National Museum of Natural History); Comal Co., New Braunfels, 12-III-72, 1 ♂ (genitalia on slide AB 4920 and represented in Figs. 3, 4) collected by A. & M. E. Blanchard.

Remarks.—This new species appears to be confined to the Edwards' Plateau region of Texas and is apparently rare. The wing pattern is somewhat similar to that of *Drepanulatrix unicalcaria* (Gn), but the course of the subterminal line is different and in the authors' series of *unicalcaria* from trans-Pecos Texas, the ground color varies from gray brown to yellowish, but not the reddish or purplish tints of *garneri*. The male genitalia are somewhat similar to those of *D. hultii* (Dyar), but that species lacks a costal process on the valves. The female genitalia are not closely similar to any described *Drepanulatrix* species. The new species is named for the principal type locality, Garner State Park, one of the most beautiful and popular parks in the state and dedicated to John Nance Garner, thirty-second vice president of the United States.

***Tarachidia septuosa*, Blanchard & Knudson, NEW SPECIES**

Figs. 7-13

Male and female.—*Head*: Front bulging, smooth, with clypeus a slightly raised ridge, clothed with flatly appressed pale brownish-ochreous (buff colored) scales; vertex rough scaled, buff; labial palpi ascending barely exceeding front, buff colored with dark brown bands at bases of 2nd and 3rd segments; antennae simple, scape light buff, flagellum scaled dorsally with pale buff and fuscous bands on each segment, ventrally bearing numerous short fine setae in male, sparsely setose in female. Thorax buff colored above and beneath; fore and mid tibiae and tarsi heavily irrorated with fuscous, with whitish bands at the joints; hind leg entirely pale buff. Abdomen dull olivaceous brown. *Forewings*: Both sexes alike. Ground color light buff irrorated with fuscous, especially along costal margin; from dorsal margin at basal $\frac{1}{4}$, is a broad, oblique, olivaceous brown fascia, angled towards apex, but weakened or interrupted over cell; postmedial band of the same color, broad and diffuse, outwardly convex just beyond cell; reniform represented as an olivaceous brown spot at apex of cell, blending with postmedial band. At basal $\frac{1}{3}$ of costal margin is a diffuse, dull olivaceous brown spot; terminal line black, very thin; fringe pale buff with dull olivaceous brown spots at tornus and apical $\frac{1}{3}$. When fresh, specimens tend to have a definite greenish cast, which later fades. *Hindwings*: Fuscous, paler towards anal margin, fringe buff. *Length of forewing*: males: $n = 5$, 7.1–8.0 mm, average 7.5 mm; female: $n = 1$, 8.1 mm. *Wing venation* (Fig. 13): Forewing: 12 veins; R2 from accessory cell; stalk of R3–R4 connate with R5 from apex of accessory cell. Hindwing: 8 veins, M2 weak. *Male genitalia* (Figs. 9–11): Uncus straight, pointed, moderately setose, somewhat obscured by manica in Fig. 9; valves with elongate, curved clasper, extending nearly to apex; aedeagus nearly equal to combined lengths of uncus, tegumen and viculum, containing two strong, thorn-like cornuti. Eighth abdominal segment represented in Fig. 11, sternite on right. *Female genitalia* (Fig. 12): Papillae anales membranous, broad, moderately setose; apophyses posteriores slightly longer than apophyses



Figs. 7-13. *Tarachidia septuosa*. 7, Holotype male. 8, Paratype female. 9, Male genitalia, aedeagus removed. 10, Aedeagus. 11, Eighth abdominal segment. 12, Female genitalia. 13, Wing venation. Segment = 1 mm.

anteriores; sterigma consists of thickened and medially fused eighth segment sclerite, with well sclerotized lateral processes extending anteriorly behind ostial chamber; ductus bursae membranous, short; corpus bursae ovoid, with a large central patch of fine, thorn-like scobinations; ductus seminalis from anterior end of bursa.

Types.—*Holotype* (Fig. 7): ♂, Texas, Cameron Co., Laguna Atascosa, 16-V-74, genitalia on slide AB 3557, collected by A. & M. E. Blanchard and deposited in the National Museum of Natural History. *Paratypes*: Same county, Palmito Hill, 10 miles east of Brownsville, 13-X-79, 3 ♂ (genitalia of two on slides ECK 1032 and 1057, the former represented in Figs. 9, 10, the latter in Fig. 11; wings on

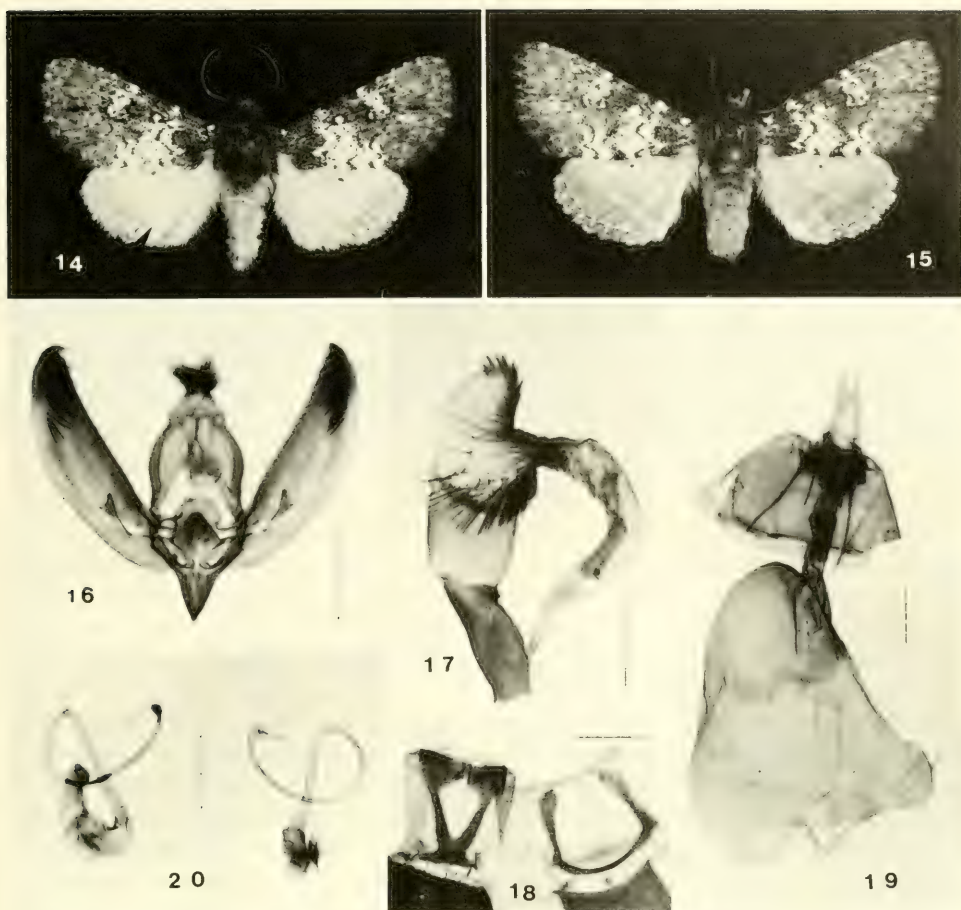
slide ECK 1115, represented in Fig. 13); Hidalgo Co., Santa Ana National Wildlife Refuge, 13-IX-80, 1 ♂; 21-X-84, 1 ♀ (in Fig. 8), genitalia on slide ECK 1049 (in Fig. 11), all collected by E. C. Knudson. One male paratype from Laguna Atascosa and the female paratype are deposited in the NMNH, others retained by collector.

Remarks.—This somber little species somewhat resembles a *Spragueia* in outward appearance, but the wing venation, front, and genitalia are more characteristic of *Tarachidia*, as currently classified. It is also somewhat similar to *Tarachidia parvula* (Walker), but that species lacks all traces of contrasting wing markings and has different genitalia.

***Paramiana exulta* Blanchard & Knudson, NEW SPECIES**

Figs. 14–20

Male and female.—*Head*: Front moderately bulging with low median keel and prominent shelf-like clypeus, clothed with flatly appressed, dark brown and pale ochreous scales, the lighter scales predominating toward the middle. Above clypeus is a blackish triangle of slightly raised scales. Vertex rough scaled, light brownish-ochreous. Labial palpi dorso-laterally dark brown, scales white tipped; medially light brown. Antennae simple; scape brown and ochreous dorsally, whitish ventrally; flagellum with each segment banded with whitish and dark brown dorsally, minutely setose ventrally. Thorax medium brown, clothed with a mixture of spatulate and hair-like scales, in a jumbled mixture of ochreous, brown, and blackish. Posterior tuft broad, but hardly elevated. Undersurface light brownish-ochreous; tibiae and tarsi dark brown, banded with whitish at joints. Abdomen light brownish-ochreous with moderate dorsal tuft on 1st segment. *Forewings*. Upper surface dark brown with conspicuous bluish white patch occupying middle $\frac{1}{3}$ of dorsal margin and extending narrowly to costal margin basad of antemedial line. Basal half line black, enclosing some bluish-white scales at extreme base. Antemedial band from costal margin at basal $\frac{1}{4}$, strongly sinuate to dorsal margin at $\frac{1}{3}$ the distance from base, inner and outer elements black, enclosing bluish-white center. Median line black, strongly sinuate and conspicuous only over pale dorsal patch. Postmedial line black, strongly dentate on veins; from costal margin at $\frac{2}{3}$ the distance from base, outwardly convex beyond cell, and to dorsal margin at $\frac{2}{3}$ the distance from base, lying just within pale dorsal patch. Orbicular round, bluish white, ringed with black. Reniform medially constricted, bluish white pupilled with blackish in upper and lower portions and ringed with black. Opposite reniform is a squarish, dull white costal spot followed by four tiny, evenly spaced, white costal spots. Subterminal line obscure, serrate, blackish, extending from outermost costal white spot towards tornus, where it disappears. Over middle of subterminal space, between M2 and M3, is a thin black dash. Termen with black intervenular dots. Fringe checkered, light and dark brown. *Hindwing*: Buff colored, suffused with fuscous along outer $\frac{1}{3}$; postmedial line fuscous, obscure above, but well defined on undersurface. Fringe buff colored. *Length of forewing*: Males: $n = 7$, 15.7–17.2 mm, average 16.2 mm; females: $n = 5$, 16.3–18.1 mm, average 16.9 mm. *Male genitalia* (Figs. 16–18): Uncus elongate, pointed, heavily setose; valves with short, blunt clasper near base, apices clothed with heavy, spinose, hairlike setae; aedeagus short and broad, about $\frac{1}{2}$ the combined length of uncus, tegumen, and vinculum; vesica rather broad, scobinate on basal $\frac{1}{3}$; a row of many long spine-like cornuti at middle; a short row of shorter cornuti at apex. Eighth ab-



Figs. 14–20. *Paramiana exculta*. 14, Holotype male. 15, Paratype female. 16, Male genitalia, aedeagus removed. 17, Aedeagus with inflated vesica. 18, Eighth abdominal segment. 19, Female genitalia. 20, Spermatophores. Segment = 1 mm.

dominal segment represented in Fig. 18, sternite on right. *Female genitalia* (Figs. 19, 20): Papillae anales membranous, sparsely setose; apophyses anteriores and posteriores about equal in length; eighth segment sclerite a broad sclerotized ring; ventral wall of ostium membranous, broadly funnel shaped; ductus bursae membranous; corpus bursae membranous, without signum, ductus seminalis arising at anterior end. Spermatophores recovered from bursa in Fig. 19 represented in Fig. 20.

Types.—*Holotype* (Fig. 14): ♂, Texas, Jeff Davis Co., Mt. Locke, 20-VIII-84, collected by E. C. Knudson and deposited in the National Museum of Natural History. *Paratypes*: Same data, 3 ♂ (genitalia of two on slides ECK 1031 and ECK 1034, the latter represented in Figs. 16–18), 2 ♀ (one represented in Fig. 15, the other with genitalia on slide ECK 1040, represented in Figs. 19, 20; same locality, 27-VIII-70, 2 ♂, 1 ♀, collected by A. & M. E. Blanchard; same county, Ft. Davis, 24-VIII-67, 1 ♂, collected by A. & M. E. Blanchard; same county, Davis Mountains State Park, 1-IX-75, 1 ♀; 19-VIII-84, 1 ♂, collected by E. C. Knudson. One ♂ and

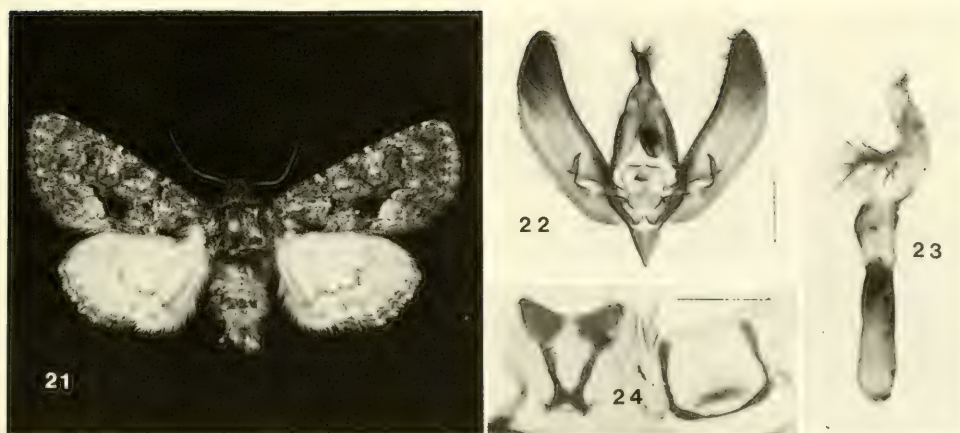
one ♀ paratype from Knudson collection donated to NMNH, and one ♂ donated to the American Museum of Natural History, others retained by collectors.

Remarks.—This striking moth appears to be confined to the Davis Mountains of Texas and is less common than the four other *Paramiana* species occurring in the same area. The moth is superficially similar to *Euamiana contrasta* (Barnes & McDunnough), from southern Arizona. This species differs from *P. exculta* in the presence of a frontal protuberance and also in pattern. In *E. contrasta*, the contrasting color is pure white, and it extends along the postmedial line to costal margin; the orbicular also has a dark center.

***Euamiana adusta*, Blanchard & Knudson, NEW SPECIES**

Figs. 21–24

Male.—*Head*: Front slightly bulging with small median tubercle, clypeus hardly projecting; clothed with closely appressed dark brown scales. Vertex clothed with erect, hair-like dark brown scales, tipped with whitish. Labial palpi ascending, not reaching middle of front, blackish brown, many scales white tipped. Antennae simple, minutely setose ventrally, scape whitish, flagellum brown. Thorax. Collar, tegulae and mesonotum clothed with mixture of hair-like and forked, spatulate scales, blackish brown, with many scales white tipped; posterior tuft inconspicuous. Beneath, clothed with long hair-like pale ochreous scales; legs tibiae and tarsi blackish brown with pale ochreous bands at joints; tibiae with massive grayish brown scale tufts. Abdomen brown, scales white tipped, no mid-dorsal tuft. *Forewing*: Predominant shade dark brown, consisting of a mixture of scales in various shades of brown, buff, and black. Basal half line absent; area basad of antemedial line somewhat suffused with dull coppery brown and buff scales, especially at middle; at dorsal margin an elongate patch of black scales extends from near base to just short of antemedial line. Antemedial line from dorsal margin at basal $\frac{1}{3}$, black, somewhat interrupted on veins, with an outwardly directed cusp over lower $\frac{1}{3}$; reaching costal margin at basal $\frac{1}{4}$. Orbicular and reniform hardly contrasted against ground color; orbicular round, ringed with black, center slightly suffused with whitish; reniform elongate, slightly medially constricted, otherwise like orbicular. Above reniform is a small whitish costal spot. Postmedial line from dorsal margin at basal $\frac{2}{3}$, black, consisting of outwardly directed lunules, the largest of which, over the lower fold, is preceded by a prominent black patch. Subterminal space suffused with coppery brown, but not strongly contrasted. Along outer $\frac{1}{3}$ of costal margin are 4 tiny, evenly spaced white dots, the obscure, sinuate, subterminal line beginning at the outermost costal dot. Termen with black, intervenular dots. Fringe with a dark line at base, outwardly slightly checkered light and dark brown and somewhat crenulate. *Hindwing*: Buff colored, weakly irrorated with dark brown along outer $\frac{1}{3}$. Subterminal line dark brown, sinuate, not reaching costal margin. Terminal line dark brown, somewhat interrupted at veins. Fringe with dark line at base, externally brownish-buff. Undersurface with prominent subterminal line and dark shade along outer margin. Length of forewing, $n = 2$, 16.4 and 17.0 mm. *Female*: unknown. *Male genitalia* (Figs. 22–24): Uncus tapered to a blunt point, heavily setose; valves with short, pointed clasper, apices of valves clothed with fine, hair-like setae; aedeagus moderately elongate, $\frac{3}{4}$ the combined length of uncus, tegumen, vinculum; vesica expanded in central $\frac{1}{3}$, armed with a



Figs. 21-24. *Euamiana adusta*. 21, Holotype male. 22, Male genitalia, aedeagus removed. 23, Aedeagus with inflated vesica. 24, Eighth abdominal segment. Segment = 1 mm.

row of innumerable long, spine-like cornuti. Eighth abdominal segments represented in Fig. 24, sternite on the right.

Types.—*Holotype* (Fig. 21): ♂, Texas, Jeff Davis Co., Davis Mts., Madera Canyon, 17-VIII-84, collected by E. C. Knudson and deposited in the National Museum of Natural History. *Paratype*: same data, 1 ♂ (genitalia on slide ECK 1044 and represented in Figs. 22-24), retained by collector.

Remarks.—This species is known only from two males collected in Madera Canyon (not to be confused with the celebrated Arizona canyon of the same name). It is superficially closest to *Euamiana dissimilis* (Barnes & McDunnough), but in that species, which has not been collected in Texas, the subterminal area of the forewing is distinctly lighter than the median area and the vesica of the aedeagus in *E. dissimilis* has short stubby basal spines and a stout apical spine.

ACKNOWLEDGMENTS

We are grateful to Robert W. Poole, Systematic Entomology Laboratory, Washington, D.C. for examining some of the type material, reviewing the manuscript, and providing comparative remarks for the new *Paramiana* and *Euamiana*. We also acknowledge the cooperation and assistance of officials of Texas Parks and Wildlife Dept., The McDonald Observatory, and Santa Ana and Laguna Atascosa National Wildlife Refuges.

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**TRICHOGRAMMA NOMLAKI PINTO AND OATMAN
(HYMENOPTERA: TRICHOGRAMMATIDAE): A REINTERPRETATION
OF GENITALIC HOMOLOGIES AND NEW
DISTRIBUTION RECORDS**

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Abstract.—*Trichogramma nomlaki* Pinto and Oatman was recently described from a single male collected in northern California. Additional specimens now available from Alberta and North Carolina indicate that certain structures of the highly distinctive male genitalia were incorrectly interpreted in the original description. The genital capsule of a male from North Carolina is figured and labelled to indicate correct homologies. A discussion of intraspecific variation is included.

Trichogramma nomlaki was described recently from a single male swept from riparian vegetation in western Glenn County, northern California (Pinto and Oatman, 1985). As stated in the original description, male genitalic structure of this species is the most highly modified yet reported in *Trichogramma*. Because of this uniqueness and the fact that only one specimen was available, homologies were considered tentative.

Two additional collections of this species are now known. Two males and one female were recently reared by one of us (M.S.T.) from Hemerobiidae eggs collected 16 July 1984 from leaves of field corn, 15 km SW of Raleigh, Wake County, North Carolina. Also, a single male was taken at Waterton Lakes National Park, Alberta, at 1300 m elevation, by sweeping "birch-fir-poplar" on 20 June 1980 (W. Mason collr.). The genitalia of all additional males are more clearly visible than in the holotype. Examination of these specimens indicates that certain homologies originally suggested were incorrect.

The genital capsule of one of the North Carolina males is illustrated and labelled in Fig. 1. In the original description of *T. nomlaki*, the dorsal expansion of the gonobase (DEG) was described as reduced and lacking a posteromedial extension. The chelate structures (CS) were considered apparently bilobed and extending further posteriorly than all other genital structures (Pinto and Oatman, 1985). This error was due to a narrow dorsal fold at the base of the DEG being misinterpreted as the entire structure. A corrected description of the genital capsule is as follows:

DEG extremely broad and elongate, not notched laterally, with posterior extension deeply, broadly emarginate apically, moderately constricted at base, extending beyond apex of CS and gonostyli (GS); CS dorsolateral to GS, well scler-

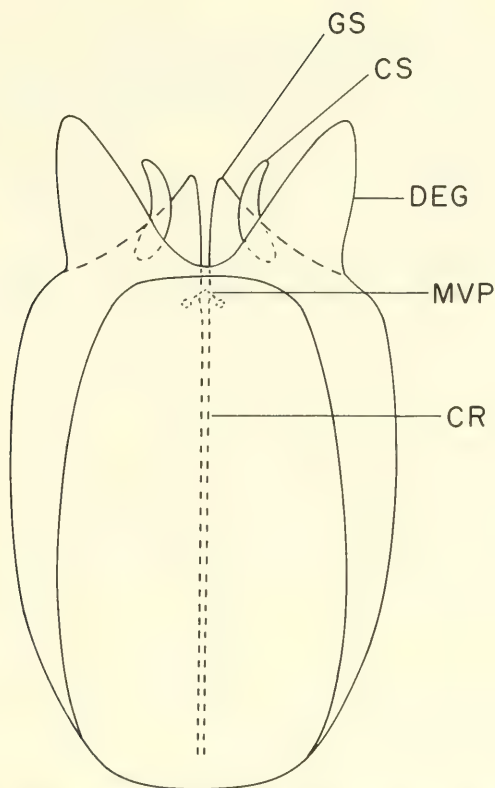


Fig. 1. Male genital capsule of *Trichogramma nomlaki* (dorsal view) from near Raleigh, North Carolina. See text for explanation of abbreviations.

otized, falciform, apex directed posterolaterally, attaining 0.95 (0.94–0.96) length of genital capsule, apical spine not apparent; GS ventromedial to CS, narrowly separated, attaining 0.92 (0.91–0.93) length of genital capsule; median ventral projection (MVP) poorly developed; chitinized ridge (CR) well developed, extending from MVP to base of genital capsule.

The genital capsule of both North Carolina males is somewhat more elongate than that of the holotype, measuring 0.55 and 0.57 as wide as long, respectively. In the male from Alberta it is similar to the holotype—0.67 as wide as long.

All other differences between the new material and the holotype also are minor. In the latter and the male from Alberta the anterior mesoscutellar setae are subequal in length to the posterior pair. In the North Carolina material they are shorter, varying from 0.6–0.8 the length of the posterior pair. Also, the number of setae between the vein tracts of the fore wing differ. For example, in the holotype and the Alberta male there are 43 and ca. 55 setae between the 4th and 5th tracts, respectively; in the North Carolina specimens the number varies from 14–18. The Alberta male has shorter flagellar setae, the longest being only ca. 1.6 the greatest flagellar width. In the other males this ratio varies from 2.2–2.5

Considering the distance between the collections of *T. nomlaki* and the paucity of material, we presently do not view this variation to be taxonomically significant.

Except for the length of the antennal setae, the holotype is more similar to the Alberta male than to the North Carolina specimens.

The single female specimen of *T. nomlaki* is similar to those of other *Trichogramma* in all respects. However, its ovipositor is shorter than most, measuring only 0.75 the length of the hind tibia.

The broad apically emarginate posterior extension of the DEG separates *T. nomlaki* from all other described *Trichogramma*. This species was originally considered closest to *T. atopovirilia* Oatman and Platner on the basis of DEG structure. Our reinterpretation of this character indicates closer relationship to *T. drepanophorum*, recently described from Mississippi (Pinto and Oatman, 1985). As in *T. nomlaki* the DEG is very broad and elongate in *T. drepanophorum* but not apically emarginate. Also, the CR is well developed, and the CS are similar. They are curved in both species with the apex directed posterolaterally rather than posteriorly as in most *Trichogramma*.

ACKNOWLEDGMENTS

Fig. 1 was prepared by Patricia Mote. The sweep sample containing the specimen from Alberta was made available to us by Carl Yoshimoto of the Biosystematics Research Institute, Ottawa. This study was supported in part by Grant BSR-8415378 from the National Science Foundation (JDP, Principal Investigator).

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A NEW OAK-MINING ERIOCRANIID MOTH FROM
SOUTHEASTERN UNITED STATES
(LEPIDOPTERA: ERIOCRANIIDAE)

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Abstract.—Adult and larval stages of *Eriocraniella* (*Disfurecula*) *mediabulla* Davis, new species, are described and illustrated. Adult moths have been collected in northern Georgia, northern Florida, southern Louisiana, and northeast Texas. The larva mines new leaves of *Quercus nigra* L. and *Q. falcata* Michx. and probably also *Q. alba* L., *Q. hemisphaerica* Bartr., and *Q. virginiana* Mill.

Recent fieldwork in southeastern United States by several collaborators has revealed the presence of a new species of Eriocraniidae. The discovery marks the first record of the endemic North American genus *Eriocraniella* from southeastern United States and only the second species of this genus found east of the Great Plains. It is also the first eastern North American record of the subgenus *Disfurecula*.

The plant hosts of all members of *Eriocraniella* whose larval biology is known are restricted to *Quercus* (Davis, 1978). *Eriocraniella mediabulla*, new species, appears to feed on a rather broad range of *Quercus*. It is known to feed on black oak (*Q. nigra*) and is suspected to feed on other oaks of both the red and white groups.

Deposition of specimens referred to in this paper are: ECK for Collection of Edward C. Knudson, Bellaire, Texas; JBH, Collection of John B. Heppner, Gainesville, Florida; UCB, University of California, Berkeley, California; USNM, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C.; and VAB, Collection of Vernon A. Brou, Edgard, Louisiana.

Eriocraniella (*Disfurecula*) *mediabulla* Davis, NEW SPECIES

Figs. 1-24

Adult (Fig. 1).—Length of forewing: ♂, 3.8-4.1 mm; ♀, 3.3-3.7 mm. Small moths with shiny black to dark fuscous wings; forewings with a golden to bluish luster; hindwings slightly paler, more purplish.

Head: Sparsely covered with mostly white to light buff piliform scales intermixed slightly with fuscous hairs particularly along occipital ridge (from chaetosemata). Antennae approximately 0.5 the length of forewing, 29-34 segmented; scape dark fuscous to black with numerous scattered pecten; flagellum uniformly black except for few whitish setae at apex. Maxillary palpi mostly fuscous, suffused



Fig. 1. *Eriocraniella mediabulla*, ♀ paratype, length of forewing 3.8 mm.

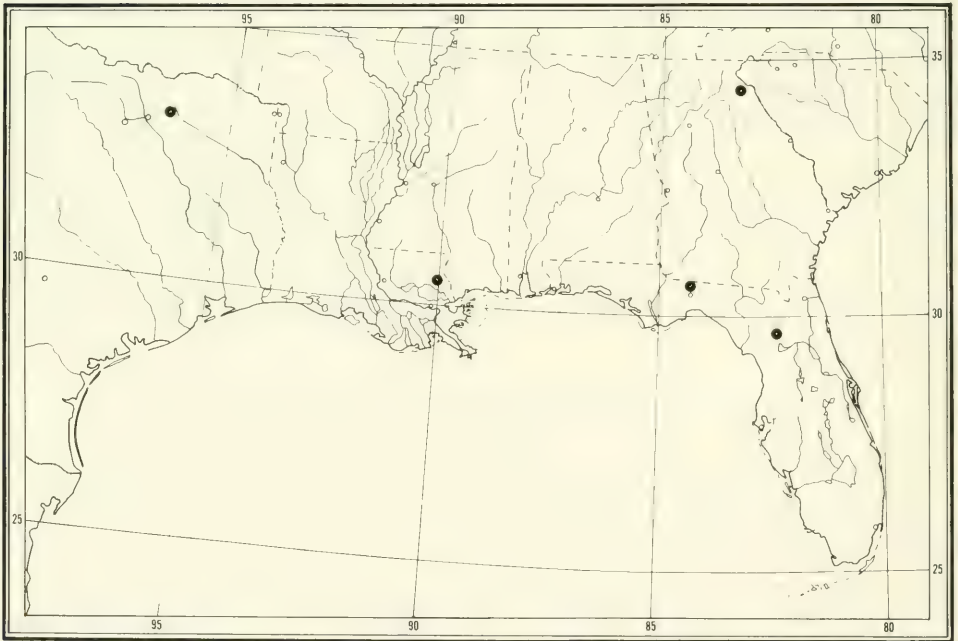
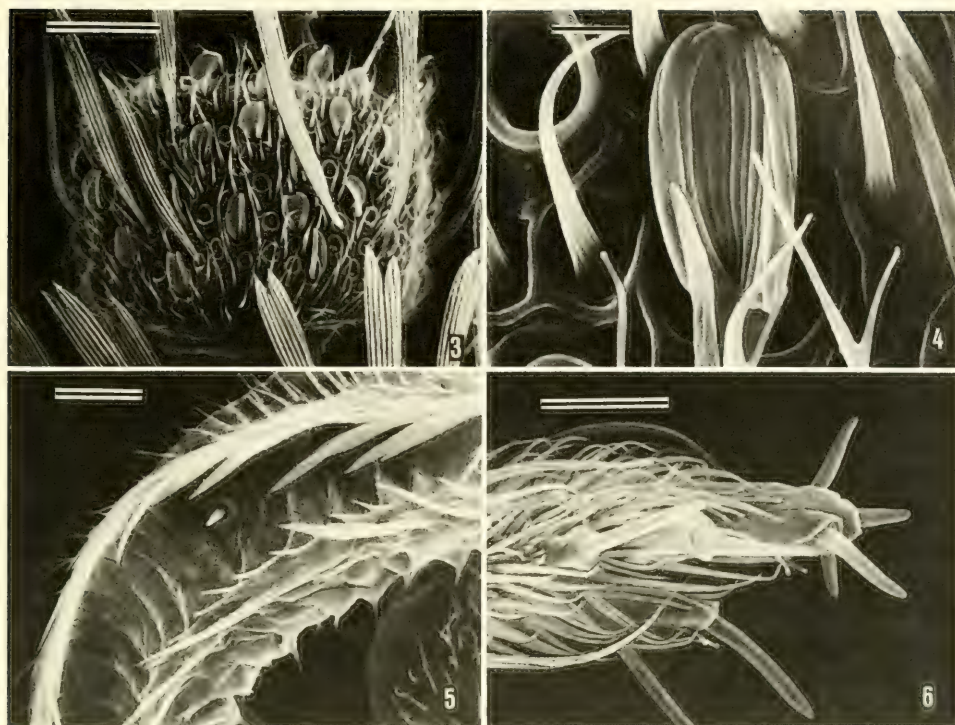


Fig. 2. Distribution of *Eriocraniella mediabulla*.



Figs. 3–6. *Eriocraniella mediabulla*, adult structure. 3, Antenual segment (scale = 20 μm). 4, Detail of sensillum aurillicum in Fig. 3 (scale = 2 μm). 5, Haustellum, inner surface of food channel (scale = 10 μm). 6, Maxillary palpus, apex of fifth segment (scale = 10 μm).

with grayish white mesally; apex with a relatively large lobe bearing four stout setae and two pairs of smaller, subapical lobes each bearing a single large seta. Labial palpi sparsely covered with grayish white scales and relatively dense brush of fuscous, piliform scales.

Thorax: Pronotum shiny black to dark fuscous. Venter sparsely covered with buff to grayish white scales. Forewings uniformly black with a distinct golden to sometimes bluish luster. Hindwings slightly paler, fuscous with a distinct purplish luster along costal half. All legs rather uniformly fuscous without distinct markings or annulations. Forelegs with epiphysis absent.

Abdomen: Sparsely covered with fuscous to buff, piliform scales. Fourth sternite of female with relatively large oval fenestrae approximately 0.4 the width of sternite; male without fenestrae. Sternal tubercles present on fifth sternite of both sexes. Eighth sternite with a conspicuous circular fenestra to left side.

Male genitalia: As shown in Figs. 8–10. Uncus shallowly bilobed; lobes rounded. Anal tube completely membranous, basal sclerites absent. Socii present, consisting of a single, relatively large seta. Caudal margin of vinculum produced to form a short, rounded medial knob with a broad base. Anterior apophyses relatively short and broad, ca. 0.3 the length of undivided vinculum. Base of aedoeagus bulbous; ventral phallic branch slightly curved and stout, nearly the diameter of

dorsal branch; base of ventral branch moderately swollen, apex with a triangular lobe.

Female genitalia: As shown in Figs. 11–13. Apex of ovipositor broadly acute as in *Eriocraniella variegata* Davis; lateral edges serrulate with 9–10 minute teeth. Bursa copulatrix moderately long, greatly exceeding cephalic apices of anterior apophyses. Walls of corpus bursa entirely membranous. Vaginal sclerite darkly sclerotized, moderately long (greatest width ca. 0.33 the length) and depressed, without median keel.

Larva (Figs. 14–24).—Length of largest larva 9 mm; diameter 1.5 mm.

Head: Uniformly light brown to stramineous with frontal sutures darkly outlined. Greatest width 0.7 mm; length 0.85. P1 reduced, approximately equal to A2, usually closer to ecdysial line than to A2. A1 and O1 absent. O2 remote from S03, closely associated instead with G1 and 2. S0 series widely separated from one another. Labrum similar to *E. xanthocara* Davis, with all setae simple and acute; anterior margin of pilifers and epipharynx densely spinose. M3 much closer to M2 than to L3. Mandibles with an inner median tuft of 8–10 elongate setae; each seta finely branched, appearing serrated.

Thorax: Pronotal and prosternal plates present but inconspicuous in preserved mature larvae (in alcohol). L2 and L3 variable in position, one sometimes more dorsal than other; L1 far forward. All three SV setae present. Legs absent.

Abdomen: Integument milky white in color. L1 present on all segments, situated relatively high above SD1 and spiracles on A1–8. SV2 absent on A1 and 8, present on A2–7. A9 similar to *Dyseriocrania griseocapitella* (Wlsm.) in possessing a complete set of 10 pairs of primary setae; both SD2 and SV2 are present and well developed. Anal plate with 2 pair of setae; bar-like sclerite (BS) present, very irregular in outline.

Holotype.—♂. Archer Road Lab, 3 mi [4.8 km] SW Gainesville, Alachua Co., Florida; 8 Mar. 1976, coll. at blacklight J. Heppner, USNM 100672.

Paratypes.—FLORIDA: Alachua Co: 1 ♀, same data as holotype (JBH); 2 mi [3.2 km] NW Gainesville: 1 ♂, 10 Mar. 1974, J. Heppner (JBH). Leon Co: Tall Timbers Research Station, 12 mi [19.2 km] N. Tallahassee: 3 ♂, 1 ♀, 17 Feb. 1978, P. Opler (USNM); 15 mi [24 km] N. Tallahassee: 1 ♂, 1 ♀, 19 Mar. 1978, E. Conner, sweeping *Quercus nigra* (USNM); 4 larvae (slides USNM 22453, 23553), 11 Apr. 1979, 1 larva, 12 Apr. 1979, ex. *Quercus falcata*, S. Faeth (USNM). GEORGIA: Franklin Co: Royston: 1 ♀, 11 Apr. 1981, Brown & Ashworth (USNM). LOUISIANA: St. Tammany Par: 4.2 mi [6.7 km] NE Abita Springs, Sec. 24, T6 SR 12E: 1 ♂, 29 Mar. 1984, V. Brou, UV trap (VAB). TEXAS: Hunt Co: Wind Point Park, lake Tawakoni: 1 ♂, 12 Mar. 1985, E. Knudson (ECK).

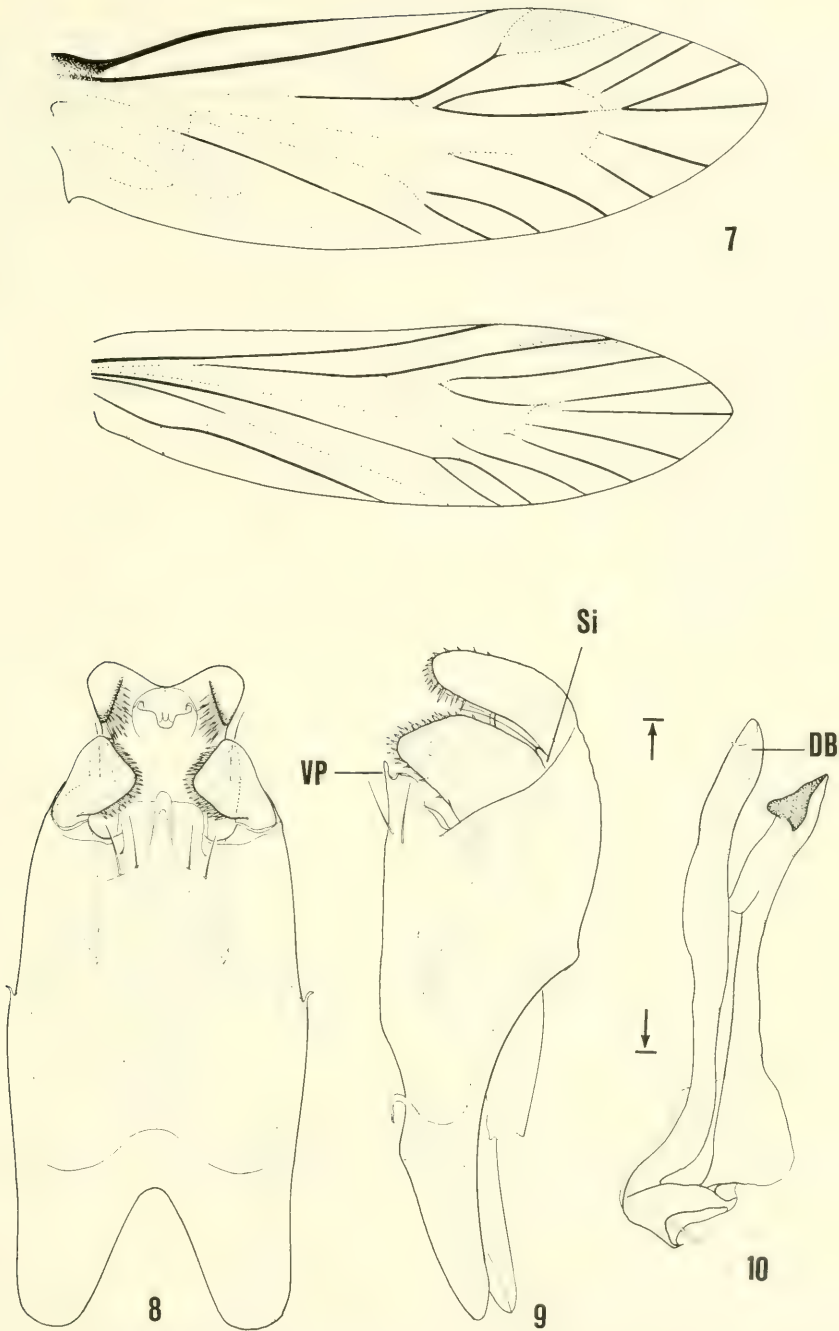
Hosts.—*Quercus nigra* L. and most probably *Quercus falcata* Michx.

Flight period.—Early March to mid April; univoltine.

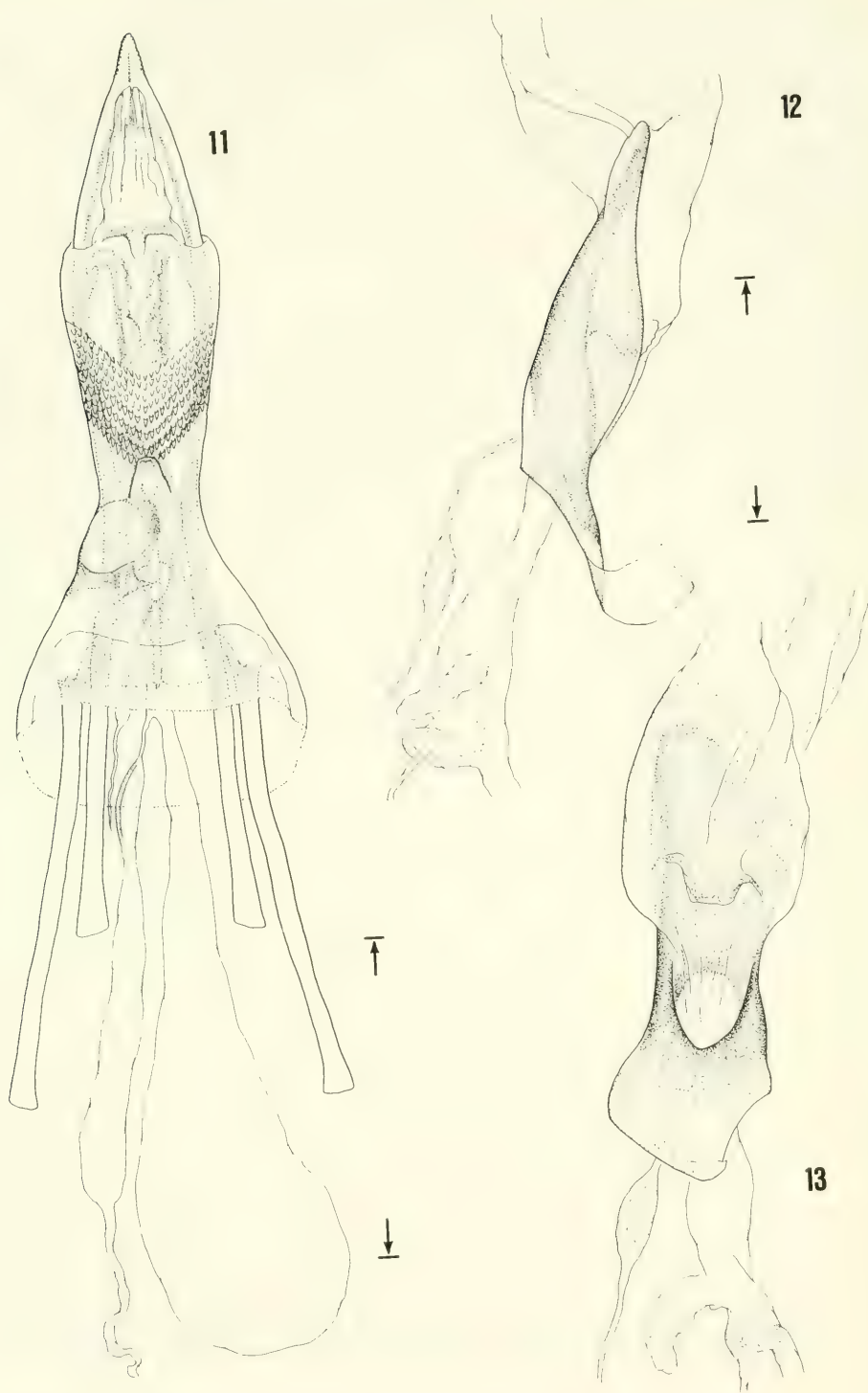
Distribution (Fig. 2).—This species ranges along the Atlantic and Gulf coastal plain from northern Georgia and Florida, west to northeast Texas.

Etymology.—The specific name is derived from the Latin *media* (middle) and *bull*a (knob) in reference to the diagnostic midventral, knoblike process on the vinculum of the male.

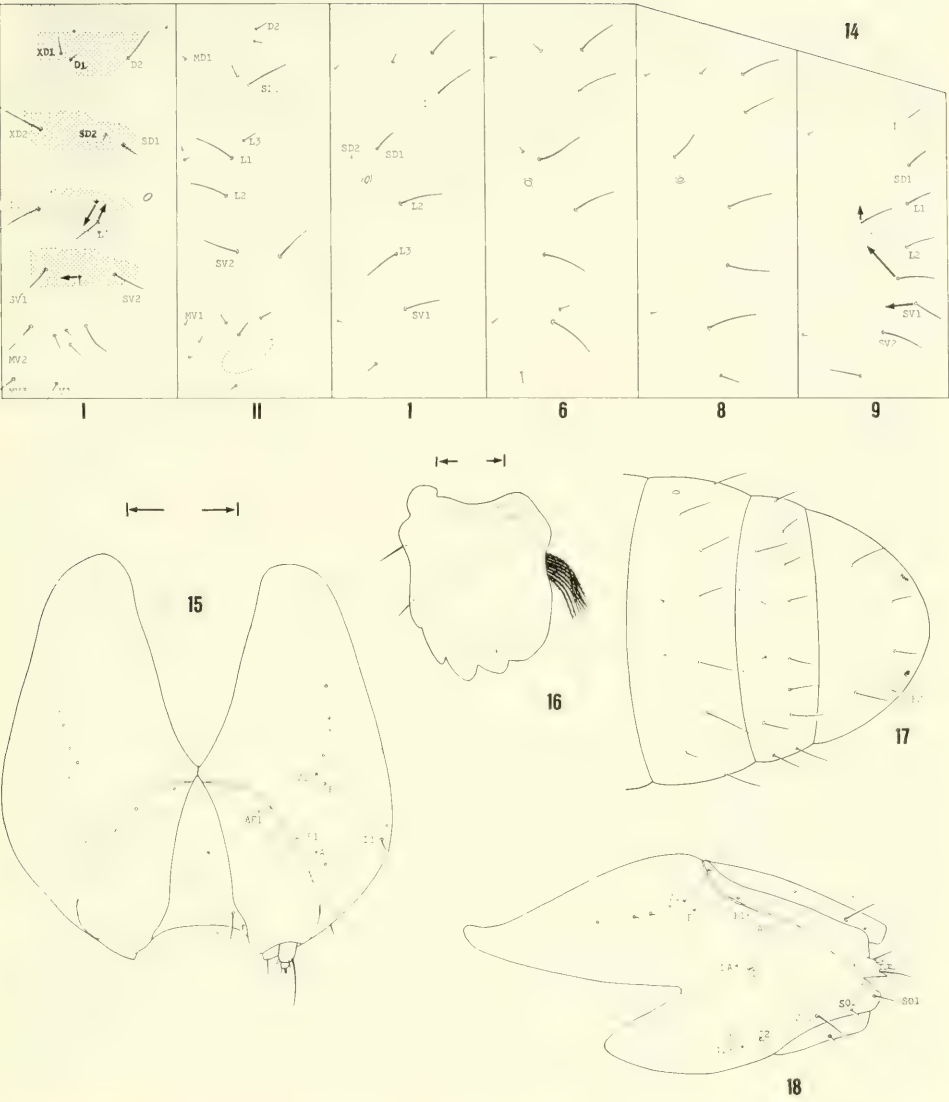
Discussion.—Both venational and maxillary palpal structures clearly indicate the generic placement of *Eriocraniella mediabulla*. Its subgeneric relationships are not so clear, although male genital morphology most strongly suggests the



Figs. 7–10. *Eriocraniella mediabulla*, adult structure. 7, Wing venation. 8, Male genitalia, ventral view. 9, Lateral view (VP = vincular process; Si = socii). 10, Aedoeagus (DB = dorsal branch; scale = 0.5 mm).



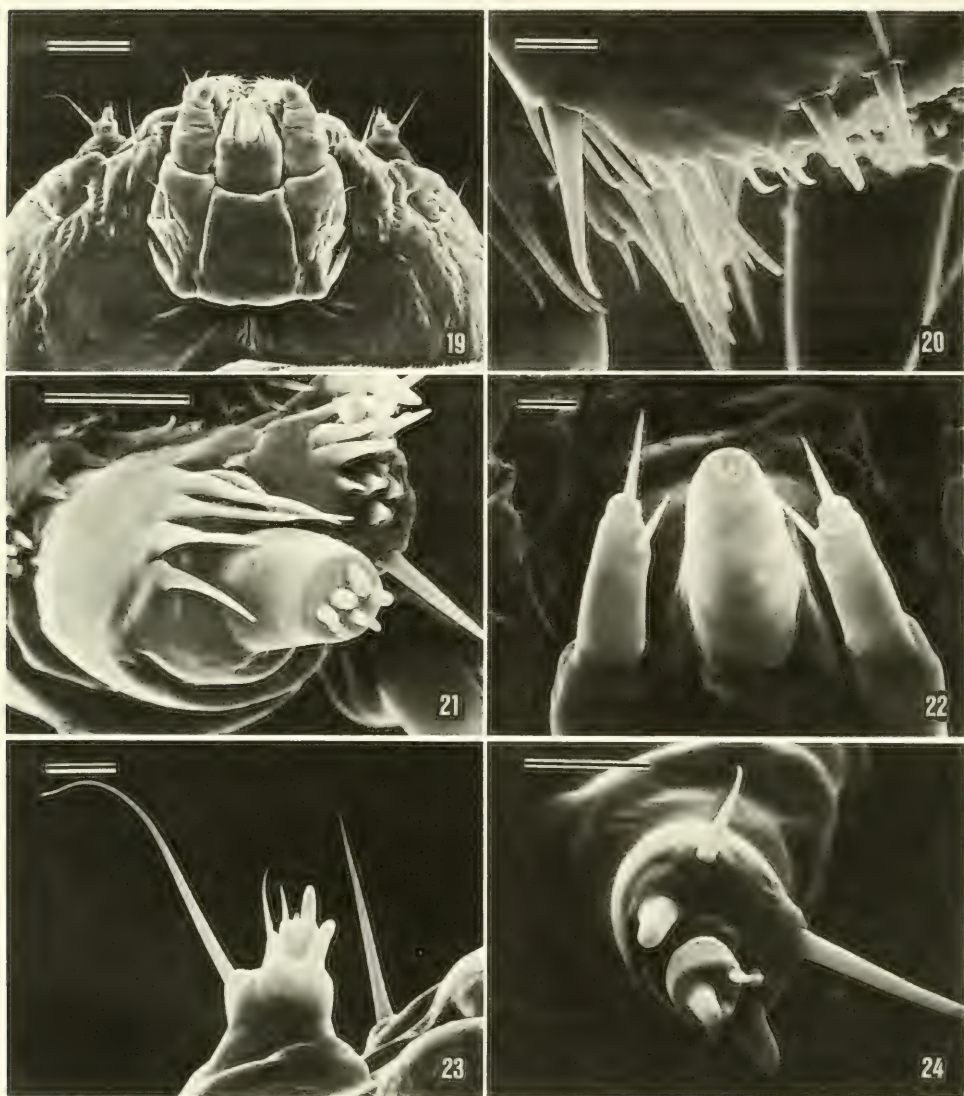
Figs. 11-13. *Eriocraniella mediabulla*, female genitalia. 11, Ventral view (scale = 0.5 mm). 12, Lateral view of vaginal sclerite (scale = 0.2 mm). 13, Ventral view of vaginal sclerite.



Figs. 14–18. *Eriocraniella mediabulla*, larval chaetotaxy. 14, Lateral schematic of prothorax, mesothorax, and abdominal segments 1, 6, 8, and 9. 15, Dorsal view of head (scale = 0.2 mm). 16, Left mandible (scale = 0.05 mm). 17, Dorsal view of abdominal segments 8–10 (BS = Bar like sclerite). 18, Lateral view of head.

subgenus *Disfurchula*. One possible contradiction to this placement is the presence of what appears to be a modified ventral pocket on A9 of the females, which in the subgenus *Eriocraniella* is lined with small spines (Davis, 1978: 27). *Eriocraniella mediabulla* differs from all other members of *Disfurchula* in lacking an epiphysis (as does *Dyseriocrania* and *Eriocrania*) and a ventral keel on the vaginal sclerite.

Although adults have yet to be reared from *Quercus falcata*, the larvae collected on this oak and figured in this paper are believed to represent *E. mediabulla*. The



Figs. 19–24. *Eriocraniella mediabulla*, larval structure. 19, Ventral view of head (scale = 10 μ m). 20, Anterior margin of right half of labrum (scale = 10 μ m). 21, Maxilla (scale = 20 μ m). 22, Spinneret and labial palpi (scale = 10 μ m). 23, Antenna, dorsal view (scale = 20 μ m). 24, Antenna, apical view (scale = 20 μ m).

most diagnostic features of the larva are the absence of the cranial setae 01 and A1 and the presence of an entire complement of 10 primary setae on the ninth abdominal segment. This species is the only eriocraniid known to have lost 01, with A1 absent also in *D. griseocapitella* (Wlsm.) and *Eriocraniella xanthocara* Davis. *Dyseriocrania griseocapitella* is the only other eriocraniid known to possess 10 primary setae on A9. The peculiar mandibular setal tuft of *E. mediabulla* also occurs in *D. griseocapitella*, *D. auricyanea* (Wlsm.), and *E. xanthocara*.

Biological observations.—Biology of this species is based upon observations of larvae and adults in the field. It has been reared from *Quercus nigra* and, on the

basis of leaf mine collections, probably also feeds on *Q. hemisphaerica*, *Q. falcata*, *Q. alba*, and *Q. virginiana* in north Florida. Eggs are inserted near the edge of leaves of *Q. nigra*, usually beyond the distal half, and only in leaves of newly emerging buds approximately in mid-March. Although *Q. nigra* and other likely host oaks in northern Florida can produce secondary flushes of new leaves in late summer, this species has not been found on secondary flushes, suggesting it is strictly univoltine, as are all other Eriocraniidae. Eggs hatch in 7–10 days.

The larva begins a serpentine mine in the upper epidermis of the leaf, proceeding along the leaf edge to the apical portion of the leaf where a full-depth, blotch-shaped mine is produced. The mines of *E. mediabulla* differ in mine development from those of *D. griseocapitella*, the only other sympatric species of Eriocraniidae. Due to inherent differences in preferred oviposition sites, the mines of *E. mediabulla* begin more distad on the leaf than do those of *D. griseocapitella*. In the latter, the mine commences near the lower one third of the leaf and continues along the leaf edge as a serpentine mine to the distal half. In both species the serpentine mine abruptly broadens to form a large blotch near the leaf apex. Another prevalent difference between the mines of these two species is that no opening forms at the oviposition site of *E. mediabulla*. In many eriocraniids, including *D. griseocapitella*, a small, oval hole, approximately 1.5–2.0 mm in length, normally develops around the egg scar as the leaf expands. Frass is deposited in semi-circles within the blotch mine. There are probably four instars. When disturbed, the larva wriggles violently. The larva completes development rapidly, within 7–10 days, then cuts a crescent-shaped hole in the lower leaf surface, and drops to the soil surface. It then burrows into the soil and spins a cocoon. It is not known if the larva diapauses within the cocoon or immediately forms a pupa. The insect remains in the soil as either a diapaused larva or a pupa until the following spring.

Little is known of the pupal stage, except pupation occurs in the soil. Other eriocraniids on oak are known to pupate only after several months or more of larval diapause (Opler, 1974). Adults have been collected at the time of bud burst on buds or catkins of *Q. nigra*. The latter observation suggests the adult may feed on pollen (Opler, pers. comm.).

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NEW SYNONYMY IN CARIBBEAN ANTS OF THE GENUS
LEPTOTHORAX (HYMENOPTERA: FORMICIDAE)

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Abstract.—The neotropical genus *Macromischa* is formally recognized as a synonym of *Leptothorax*. The following new species-group synonymy is proposed. *Leptothorax isabellae* (Wheeler) [= *Macromischa isabellae* var. *muticus* M. Smith = *L. (Macromischa) hyperisabellae* Baroni Urbani]; *L. laeta* (Wheeler) [= *M. affinis* Mayr, preoccupied, = *L. (M.) similis* Baroni Urbani]; *L. villarensis* (Aguayo) [= *M. manni* wheeler, preoccupied, = *L. (M.) williamsi* Baroni Urbani].

Macromischa was originally described as a genus allied to *Leptothorax* Mayr, 1855, by Roger, 1863. Mann (1920) divided *Macromischa* into three subgenera when he proposed two new subgenera, *Croesomyrmex* and *Antillaemyrmex*. Although "typical" *Macromischa* are very distinctive ants with a unique habitus, there are several species in Central America and northern South America, mostly undescribed, that effectively bridge the gap between *Macromischa* and the genus *Leptothorax*. Baroni Urbani (1978) correctly recognized the problem when he proposed to reduce *Macromischa* to subgeneric status. More recently, Bolton (1982) expressed the opinion that "... *Macromischa* is best regarded as a synonym of *Leptothorax*," but did not formally synonymize it. Therefore, I formally propose to treat *Macromischa*, and its included synonyms *Croesomyrmex* and *Antillaemyrmex*, as a synonym of *Leptothorax* (NEW SYNONYMY).

The transfer of *Macromischa* to *Leptothorax*, as proposed by Baroni Urbani, had the predictable result that a number of names were preoccupied. For those that were not synonyms, Baroni Urbani proposed new names. There are two instances, however, in which he erred by proposing new names for which there were earlier names available. These two cases are corrected below.

Leptothorax laetus (Wheeler)

Macromischa affinis Mann, 1920: 417; ♀. Preoccupied in *Leptothorax* by *L. affinis* Mayr, 1855: 442.

Macromischa affinis subsp. *laeta* Wheeler, 1937: 456; ♀.

Macromischa affinis subsp. *moerens* Wheeler, 1937: 456; ♀.

Leptothorax (Macromischa) similis Baroni Urbani, 1978: 501. Unnecessarily proposed to replace *L. affinis* (Mann, 1920). NEW SYNONYMY.

Discussion.—Both of the names proposed by Wheeler are available and either may be used. Since *M. laeta* was the first described, I have chosen to use that

name. I have examined cotypes of all three nominate forms and agree with Baroni Urbani that they are conspecific.

***Leptothorax villarensis* (Aguayo)**

Macromischa manni Wheeler, 1931: 19; ♀. Preoccupied in *Leptothorax* by *L. manni* Wheeler, 1914.

Macromischa manni var. *villarensis* Aguayo, 1931: 177; ♀.

Leptothorax (*Macromischa*) *williamsi* Baroni Urbani, 1978: 530. Unnecessarily proposed to replace *L. manni* (Wheeler, 1931). NEW SYNONYMY.

Discussion.—Since Aguayo's name is available as the oldest valid name for this species, the replacement name proposed by Baroni Urbani is unnecessary.

***Leptothorax isabellae* (Wheeler)**

Macromischa isabellae Wheeler, 1908: 138; ♀, ♀, ♂.

Macromischa isabellae subsp. *mutica* M. Smith, 1937: 747; ♀ NEW SYNONYMY.

Leptothorax (*Macromischa*) *hyperisabellae* Baroni Urbani, 1978: 453–454; ♀ NEW SYNONYMY.

Leptothorax (*Macromischa*) *isabellae*: Baroni Urbani, 1978: 456–459; ♀, ♀, ♂.

Leptothorax (*Macromischa*) *muticus*: Baroni Urbani, 1978: 464–465; ♀.

Discussion.—This ant is generally distributed throughout forested areas of Puerto Rico. Workers of the nominate form originally described by Wheeler possess short propodeal spines. The form described by Smith was characterized by the lack of propodeal spines and subtle differences in the form of the head and thorax, and the weakly developed ventral petiolar process. Baroni Urbani's *L. hyperisabellae* is based on a single worker with unusually long propodeal spines.

Among the numerous specimens available to me is a nest series collected at Maricao, the type locality of subsp. *mutica*. Most specimens possess distinct spines, some have short denticles, and some are unarmed. The other characteristics cited by Smith are equally unsupportable and I consider subsp. *mutica* a synonym of *L. isabellae*, not a valid species as supposed by Baroni Urbani.

Another nest series, from El Yunque, the type locality of *L. hyperisabellae*, consists exclusively of workers with propodeal spines. In some, the spines are very short and denticle-like; in others they are conspicuously longer and, although none have spines as long as illustrated for *L. hyperisabellae*, are very similar to *L. hyperisabellae*. The difference is a small one of degree only and I attach no significance to it.

It should be noted that Baroni Urbani's figures of the thoraces show conspicuous differences in shapes, especially in dorsal view. The worker caste of *L. isabellae* is unusually variable because there is a pronounced tendency toward pseudogynes. Many workers possess ocelli and at least some suggestion of female-like thoracic sutures. Humeral angles may be sharp or wholly lacking. Therefore, caution is advised when considering thoracic shape in *L. isabellae*.

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**OBSERVATIONS ON SOME NESTS OF
CROSSOCERUS (BLEPHARIPUS) A. ANNULIPES
(LEPELETIER AND BRULLÉ) (HYMENOPTERA: SPHECIDAE)**

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Abstract.—Ten nests of *Crossocerus (Blepharipus) annulipes annulipes* found in a rotting log in Pennsylvania are described and figured. Thirty fully-provisioned cells contained from 14 to 30, mostly adult Cicadellidae per cell. Two new cicadellid hosts, *Ribautiana unca* and *Typhlocyba hockingensis*, are reported from the cells. Two cells contained nymphal Miridae and one an adult Chironomidae and nymphal Miridae in addition to the adult and nymphal cicadellid prey.

Crossocerus (Blepharipus) annulipes annulipes (Lepeletier and Brullé) is widely distributed in the Holarctic Region; in North America north of Mexico the subspecies ranges from southern Canada into Georgia and California (Krombein, 1979). The other subspecies, *C. annulipes hokkaidoensis* Tsuneki, occurs in Japan (Tsuneki, 1960). Much of the biological information available for *C. a. annulipes* has resulted from studies done in Europe (summary in Leclercq, 1954). Although there are numerous prey records for this subspecies from the United States (see Krombein, 1979), detailed descriptions and figures of the nests are lacking. Davidson and Landis (1938) first reported on the life cycle, prey and cocoon of *C. a. annulipes* (as *Crabro davidsoni* Sandhouse) in North America (Ohio). Their report includes an excellent drawing of prey placement within a cell. Krombein (1958) noted the contents, including prey, of two cells of this subspecies [as *C. ambiguus* (Dahlbom)] in Virginia. Michener (1971) described the burrow, cell and contents of a "few cells" of *C. a. annulipes* (as *C. ambiguus*) in Kansas. The above-mentioned studies indicate that the subspecies nests in abandoned insect burrows in rotting stumps and logs and structural timber.

We found ten active nests of *C. a. annulipes* in a rotting log near the base of Presque Isle State Park, Erie County, Pennsylvania. Two of the nests were located in the top and four near either end of the log. They were discovered just above 2-3 cm-high and 3-4 cm-wide piles of sawdust, indicating recent burrow enlargement (excavation). The log, 91 cm long and 17 cm in maximum diameter, lay exposed on a flat, mixed sand and gravel surface, 2.5 m from a gravelly cliff and deciduous woods.

We observed eight females of *C. a. annulipes* between July 4 and 15, 1972, entering open nests with leafhopper prey and exiting headfirst seconds later. Some of the wasps, upon leaving, made 5-10-sec-long orientation flights, 40-60 cm in

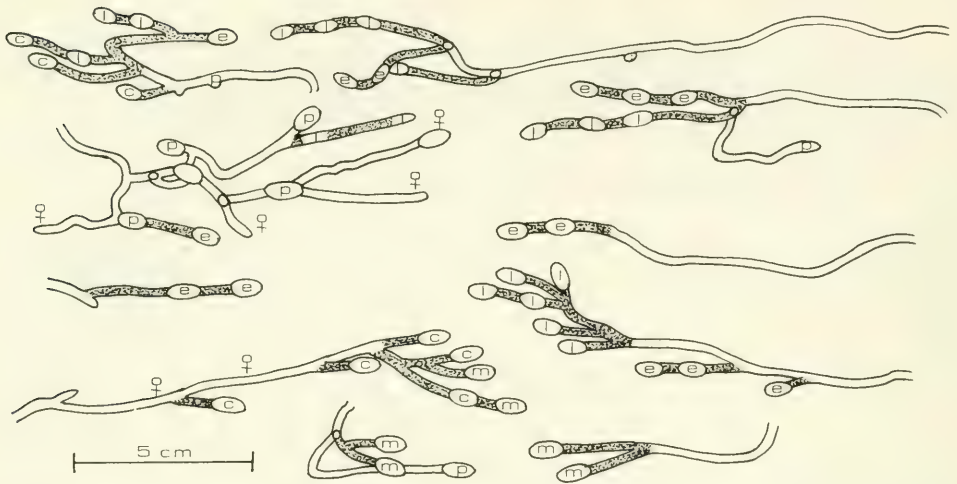


Fig. 1. Ten nests of *Crossocerus (Blepharipus) a. annulipes*, as viewed from the side. Cell contents are as follows: c, cocoon; e, egg; l, larva; m, mouldy prey; p, prey only. Stippling indicates burrow filled with sawdust and frass. ♀ shows position of collection of female(s) inside two nests. Scale refers to all nests.

length, along the long axis of the log. They then flew away rapidly and returned in flight minutes later holding the prey with the legs in a head forward position.

The burrows, 2.5–4.0 mm in diameter, entered the log at various angles to its surface but then turned abruptly or gradually and proceeded along the grain of the wood. The often elongate main burrows ranged from 2.8 to 16.0 cm in length (Fig. 1). Some of the burrows led to cells near their distal ends, whereas others gave rise to cells along most of the burrow. Not more than three cells were found in a series, each separated by sawdust and beetle frass. Some long nests contained only a few cells in series, most cells being positioned singly at the ends of short side burrows packed with sawdust and frass. One nest contained a storage chamber in the opposite direction of three cells, and other nests had prey stored in small chambers or in the burrows. In all nests the main burrow and in some the side burrows were open.

Cells ($N = 26$) containing prey and eggs, larvae or cocoons averaged 3.4 (3–4) mm wide and 8.3 (7–9) mm long. They were located roughly in the middle of the log, and were separated from neighboring cells by from 5 to 35 mm (Fig. 1). Cells containing a wasp's egg, larva or cocoon were sealed off from neighboring cells or the main burrow with sawdust and frass.

The number of prey placed in a fully-provisioned cell ranged from 14 to 30 ($\bar{x} = 21.4$, $N = 30$). Prey individuals weighed (wet) from 0.3 (nymphal cicadellid) to 2.2 (adult cicadellid) ($\bar{x} = 0.74$, $N = 268$) mg. The total weights of all prey in a fully-provisioned cell ranged from 12.6 to 22.0 ($\bar{x} = 15.86$, $N = 14$) mg. Three females of *C. a. annulipes* collected in association with nests weighed (wet) 6.9, 7.3 and 9.1 mg, respectively. (Two males collected on the log weighed only 2.9 and 3.7 mg, respectively.)

Only one cell contained adult cicadellid prey exclusively; 26 others held a preponderance of adults but also contained some nymphal Cicadellidae. Of 642 prey Cicadellidae, 470 (73%) were adults and 172 (27%) were nymphs. A sample

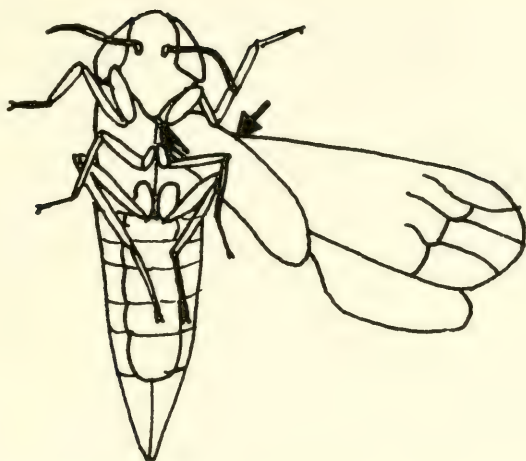


Fig. 2. Location of egg (arrow) of *Crossocerus* (*Blepharipus*) *a. annulipes* on prey Cicadellidae.

of prey Cicadellidae, all of the subfamily Typhlocybinae, is as follows: *Erythro-neura* sp., 1 ♀; *Empoa* sp., 2 ♀♀; *Empoasca fabae* (Harris), 8; *Ribautiana unca* (McAtee), 4; *Typhlocyba hockingensis* Knull, 27; and, *T. pomaria* McAtee, 2. *R. unca* and *T. hockingensis* are new prey species for *C. a. annulipes*. Two cells each contained three nymphal mirids in addition to adult and nymphal cicadellid prey, and one cell held two nymphal mirids and one adult chironomid mixed with adult and nymphal cicadellids.

Prey were "stacked" rather neatly in a cell in a mostly head inward but rather oblique position (see Davidson and Landis, 1938, Fig. 3). Rarely, one or a few prey in each cell were placed straight inward with the head against the back of the cell. The egg-bearing leafhopper was invariably positioned head inward and ventral side upward at the inner end of the cell. Of 10 such prey bearing eggs, seven were female Cicadellidae. The wasp's egg was affixed ventrally near a forecoxa, just off-center of the prey's thoracic midline (Fig. 2). The wing nearest the egg's attachment was flexed at a 60°–90° angle to the midline. One egg affixed near a left forecoxa was 1.7 mm long and 0.4 mm wide at its center.

Five cocoons removed from the cells of *C. a. annulipes* were 2.5–3.0 mm wide × 7.0–7.5 mm long. Two were covered with sawdust and beetle frass and three others contained, in addition, prey remains embedded at one end.

Two nests had more than one female wasp associated with them. One nest (RCM 2) had a female stationed head outward in the burrow, 4 cm below the entrance, and another female, 3 cm behind her in the same burrow. Both wasps had each appeared with their head inside the entrance a few minutes earlier. Another nest (FEK 1) contained four females collected at various locations within, as indicated in Fig. 1. Whether or not these females were actively participating in burrow enlargement, cell construction, and provisioning, or, were simply recent emergents from cells of a previous generation is unknown.

DISCUSSION

Crossocerus (*Blepharipus*) *annulipes* is an extremely successful species as indicated by its extensive distribution in the Holarctic Region (see Leclercq, 1954;

Krombein, 1979). This success is undoubtedly related to the wide variety of plant materials and structural timbers in which the species nests (see Leclercq, 1954, for list of plant genera). The nesting season of *C. a. annulipes* was only a little over a month old when our study site (log) was found. The daughters being reared within the cells might have utilized remaining space in the log for rearing their young until the end of the season if the log had remained in the field. An additional 40 nests could have fit easily within the remaining space of the 91×17 cm rotting log. If a finished nest contains a modest estimate of seven completed cells, as did several unfinished ones, then the log we examined could have held a total of 350 cells by season's end.

In some studies (Krombein, 1958; Michener, 1971; and the present report) the wasps appeared in part to utilize the abandoned burrows of other insects, evidently those of bees and beetles. Nevertheless only a few of the cells (never more than three) were constructed in series, indicating that the wasps must have diverged from the pre-existing insectan burrows in order to construct cells. This is totally unlike the situation in some other crabronine wasps in which most or all of the cells are built in series (see Tsuneki, 1960; Krombein, 1967; Miller and Kurczewski, 1972).

Although Davidson and Landis (1938) cited the cells of this subspecies as being $\frac{1}{4}$ – $\frac{1}{2}$ inch in length, none of the cells we excavated and measured were as short or as long as this. The cells from our study were essentially identical in width and length to those recorded by Tsuneki (1960) for *C. annulipes hokkaidoensis* (3.0 – 3.3×7.0 – 7.5 mm). The mean number of prey per cell that we found (21.4) agrees with that reported by Davidson and Landis (1938) (20.4), except that their range of 4–46 prey per cell exceeds all figures reported in the literature for either subspecies of *annulipes*.

The total weight of all prey in a cell that we recorded for *C. a. annulipes* is approximately twice that for a female wasp and more than four times that for a male wasp. Although we lack substantive data for this subspecies, it is believed that males are produced from cells containing either fewer prey or less biomass and females from cells containing more prey and biomass; at least this is the case in some other crabronine species (see Evans et al., 1980).

Studies of both subspecies of *C. annulipes* indicate a preference for adult cicadellid prey, with a preponderance of typhlocybinae leafhoppers (see Leclercq, 1954; Krombein, 1979). Although all previous nearctic studies indicate the exclusive use of typhlocybinae Cicadellidae as prey, we found that three of 30 (10%) cells contained either nymphal Miridae or nymphal Miridae and adult Chironomidae in addition to adult and nymphal leafhoppers. This corroborates the findings of Hamm and Richards (1926) and Bristowe (1948) in England.

The positions of the prey in the cells that we observed agree with those described and figured for this subspecies by Davidson and Landis (1938). Tsuneki (1960) reported similar positioning of the prey in *C. annulipes hokkaidoensis*, except that several prey were "lying in the opposite direction." Tsuneki (1960) noted two eggs of this subspecies attached to the necks of prey and then extending either obliquely across the thorax or lying parallel with the longitudinal body axis of the prey. We found eggs of *C. a. annulipes* abutted against the forecoxae of the prey but not quite reaching the cervix. In general the eggs of crabronine wasps are affixed to the cervical region of the prey, except in rare instances as in *Oxybelus*

subcornutus Cockerell where the egg is attached to the base of a forecoxa (Peckham et al., 1973). Other sphecids that prey upon leafhoppers affix the egg variously but never in the region of the throat (see Iwata, 1942; Evans, 1966; Kurczewski and Lane, 1974).

Davidson and Landis (1938) noted that the cocoons of *C. a. annulipes* consist "largely" of pieces of leafhoppers, but we did not find this to be the case. Some of the cocoons we observed contained no prey parts and others had sclerites of Cicadellidae embedded only at one end. *Bothynostethus distinctus* Fox, a larrine with many crabronine characteristics, typically covers one end of its cocoon with beetle elytra (Kurczewski and Evans, 1972).

Our observations on two nests of *C. a. annulipes*, in which we found four females in one nest and two females in another, hint at communal nesting in this species. On the other hand, these females may have been recent emergents from a previous generation which had remained with the nests. Females of *Philanthus gibbosus* (F.) remain for a while with the nests from which they have recently emerged (Evans, 1973), and those of *Cerceris* may actually overlap in generations (Salbert and Elliott, 1979; Evans and Hook, 1982). Communal nesting in the Crabroninae in which two or more females actively participate in the provisioning of a single nest has been documented for the genera *Crossocerus* (Bristowe, 1948; Peters, 1973); *Ectemnius* (Hamm and Richards, 1926; Bristowe, 1948); *Lindenius* (Miller and Kurczewski, 1973); *Moniaecera* (Evans, 1964); and *Rhopalum* (Janvier, 1928).

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TWO NEW SPECIES OF CADDISFLIES FROM GEORGIA
(TRICHOPTERA: POLYCENTROPODIDAE, HYDROPTILIDAE)

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Abstract.—Two new species of Trichoptera from a small, black water stream in central Georgia are described and illustrated. *Polycentropus thaxtoni* n. sp. (Polycentropodidae) is a member of the *confusus* species-group and *Hydroptila roberta* n. sp. (Hydroptilidae) is a member of the *consimilis* species-group.

Two new species of caddisflies were collected during an inventory of the Trichoptera of Spring Creek, Georgia. Spring Creek is a small, second order, black water stream located about five miles south-southeast of Roberta, Crawford County. Several species of southeastern caddisflies have been described from this area, including the rarely collected *Beraea gorteba* Ross (Beraeidae). The caddisfly fauna of the creek is rather diverse with 99 species in 16 families (Rothschild et al., in prep.).

Types will be deposited in the National Museum of Natural History, Smithsonian Institution (NMNH) and the Clemson University Entomological Collection (CLEM).

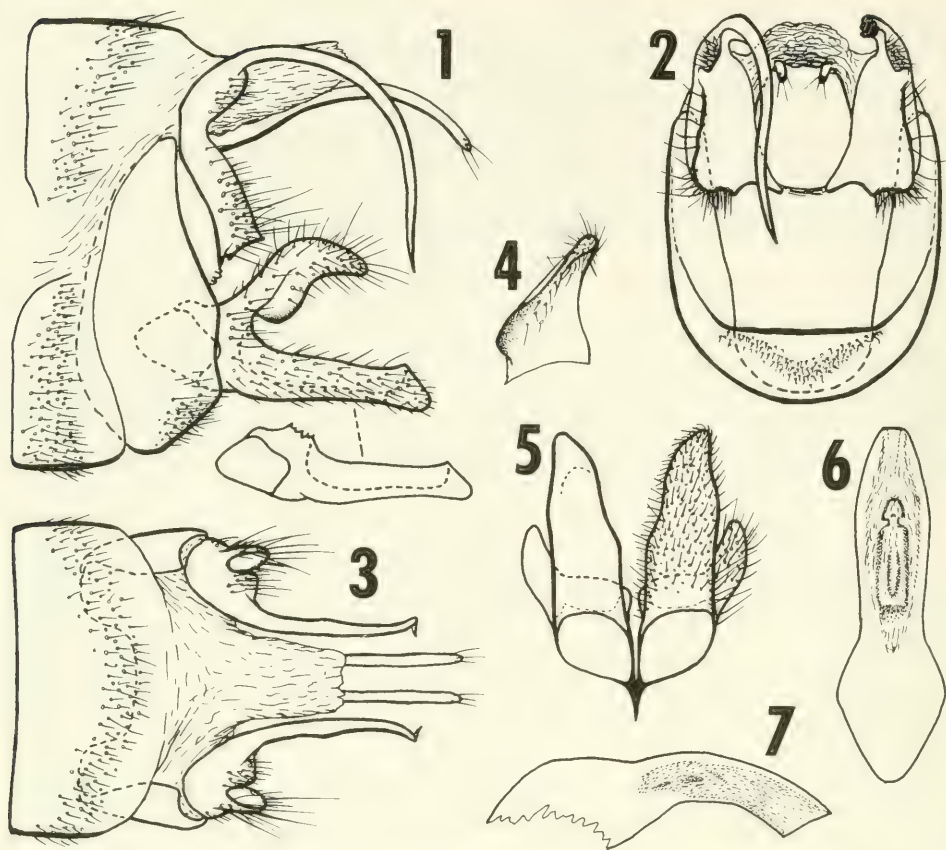
Polycentropus thaxtoni NEW SPECIES

Figs. 1-7

This species is a member of the *confusus* species-group (Ross, 1941 = *maculatus* group, Ross, 1944) of *Polycentropus sensu stricto*, members of which have the following characters: inferior appendages each with a stalked dorsobasal process; preanal appendages each with an elongate, curved dorsal portion; intermediate appendages each slightly curved, elongate, originating from the ventral surface of the otherwise membranous abdominal segment X; phallic apparatus with well developed, sclerotized phallobase, but with the remainder almost completely membranous.

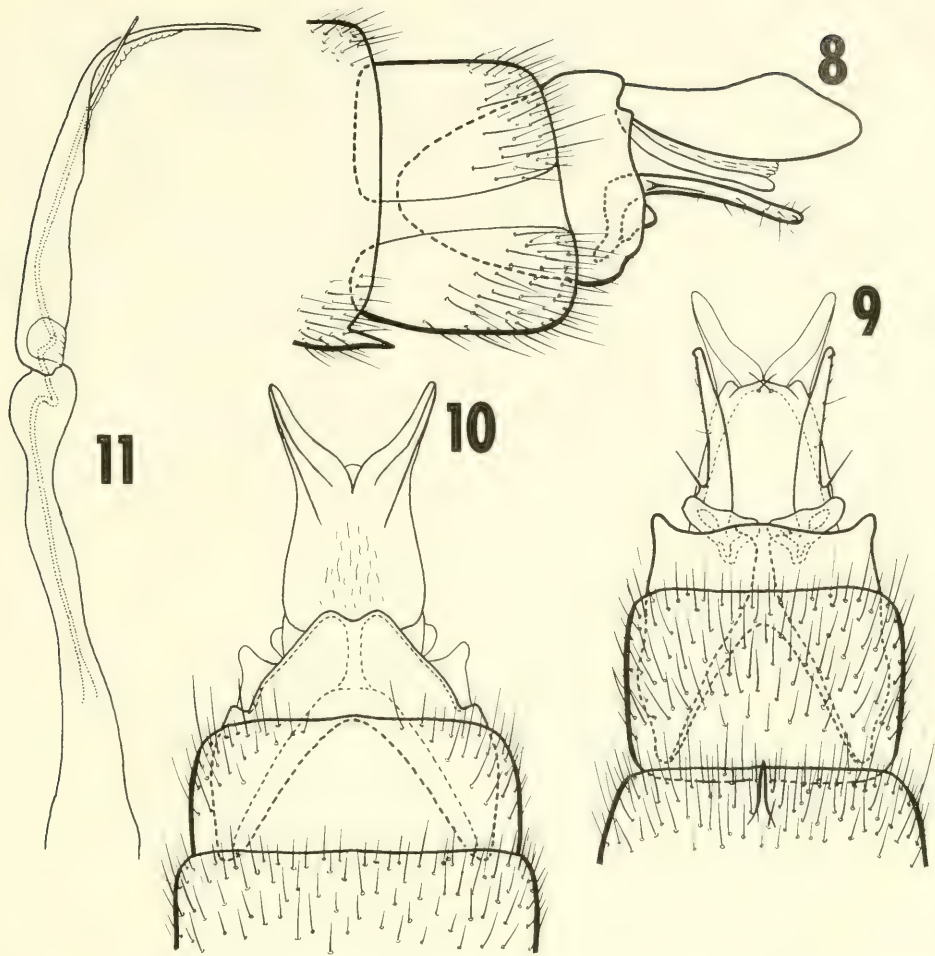
Polycentropus thaxtoni, n. sp., is most closely related to *P. chelatus* Ross and Yamamoto, *P. confusus* Hagen, *P. floridensis* Lago and Harris, *P. neiswanderi* Ross, and *P. pentus* Ross. It can be separated from these five species by the long, dorsally excavated ventral portion of each inferior appendage; the broad, posterior emargination on the basal portion of each preanal appendage; and the absence of a basoventral protuberance on the phallobase.

Male.—Length of forewing 5.9 mm. Color and structure typical for *confusus* species-group. Genitalia as in Figs. 1-7. Abdominal segment IX two-thirds height of segment VIII, narrow, acutely angled dorsally, with mesoventral patch of short



Figs. 1-7. *Polycentropus thaxtoni*, male genitalia. 1, Left lateral. 2, Posterior. 3, Dorsal. 4, Dorsobasal process of right inferior appendage, caudoventral. 5, Inferior appendages, ventral. 6, Phallic apparatus, dorsal. 7, Phallic apparatus, left lateral.

setae. Paired intermediate appendages positioned ventrally on segment X; each elongate, narrow, with apex setose, curved gradually posteroventrad. Each preanal appendage composed of basal portion and long, slender dorsal process; basal portion narrow in lateral aspect, with broad emargination just above middle, posteroventral corner pointed, posterodorsal corner broadly rounded; in posterior aspect, basal portion curved mesad below phallocrypt, but not meeting at meson; long, spine-like dorsal process evenly curved caudad, then ventrad, straightening at apex. Inferior appendages each with main, ventral portion and prominent dorsobasal process: ventral portion, in lateral aspect, nearly straight, with dorsomesal surface excavated nearly to apex; in ventral aspect, narrowed slightly distad of middle and again at apex, lateral edge slightly sinuate; dorsobasal process visible laterally in ventral aspect, in lateral aspect, with short, narrow stalk and broad, curved apical portion; in caudoventral aspect, stalk nearly as broad as greatest width of apical portion; apical portion roughly triangular with a meso-basal, darkened, rounded projection. Phallobase well developed and sclerotized; in lateral aspect with bulbous base and narrow, slightly curved apical region; basoventral protuberance lacking; remainder of phallic apparatus membranous except ejaculatory duct sclerite, retracted within phallobase.



Figs. 8–11. *Hydroptila roberta*, male genitalia. 8, Left lateral. 9, Ventral. 10, Dorsal. 11, Phallic apparatus, dorsal.

Holotype.—♂, Georgia, Crawford County, Spring Creek above pond at Camp Eunice, approx. five miles SSE of Roberta (ca. 32°40'N, 83°59'W), 8.ix.1983, S. W. Hamilton, R. W. Holzenthal (NMNH).

Paratypes.—♂, same data as holotype (CLEM); ♂, same data as holotype except, 29.ix.1983 (NMNH).

Etymology.—We take pleasure in naming this species for the late Edgar Thaxton, upon whose property it was discovered, in recognition of his generous hospitality and interest in our research.

***Hydroptila roberta* NEW SPECIES**

Figs. 8–11

This species is a member of the large *consimilis* species-group of Marshall (1979). It resembles *H. strepha* Ross, *H. quinola* Ross, *H. circangula* Harris, and *H. paralatosa* Harris in the general form of the male genitalia. The narrow, elongate, curved apex of the phallic apparatus; the protruding ejaculatory duct;

the broad, deeply cleft abdominal segment X; and the presence of apicolateral processes on the truncate subgenital plate distinguish it from other *consimilis*-group species.

Male.—Length of forewing 2.3 mm. Genitalia as in Figs. 8–11. Abdominal sternite VII with acuminate apicomesal process. Segment VIII nearly quadrate in lateral aspect, tergite slightly larger than sternite; heavily setose. Segment IX, in lateral aspect, generally triangular, about three-fourths height of VIII; with “T”-shaped, mesoventral apotome, best seen in ventral aspect. Segment X lightly sclerotized, with paired divergent apicolateral extensions; in lateral aspect, widest two-thirds distance from base. Subgenital plate two-thirds length of segment X, three-fourths length of inferior appendages; in ventral aspect, roughly trapezoidal, with short, apicolateral extensions and pair of apicomesal setae. Inferior appendage, in ventral aspect, elongate, narrow, with proximal, mesal flange and very short basolateral seta-bearing process; in lateral aspect, appendage slender, very slightly sinuate, with robust ventral flange proximally and small lateral point apically. Phallic apparatus elongate; basal portion of varying width to bulbous region next to distal portion; distal portion with apical one-third attenuated, curved; ejaculatory duct exceeding membrane, exposed portion sclerotized; paramere absent.

Holotype.—♂, Georgia, Crawford County, Spring Creek below pond at Camp Eunice, approx. 5 miles SSE of Roberta (ca. 32°40'N, 83°59'W), 5.vi.1981, S. W. Hamilton, M. Rothschild, ultraviolet light (NMNH).

Paratypes.—♂, same data as holotype, except above pond, 11.vi.1983, S. W. Hamilton, Malaise trap (CLEM); 5 ♂, same data, except above pond at old log bridge, 27.v.1983, S. W. Hamilton, R. W. Holzenthal, ultraviolet light (CLEM, NMNH); ♂, same data as 27.v.1983 paratype, except 10.vi.1983 (NMNH).

Etymology.—We name this species after the small town of Roberta, about five miles north of the type locality.

ACKNOWLEDGMENTS

We thank John C. Morse and Peter H. Adler, Clemson University, for reviewing our manuscript. We also thank Steven C. Harris, University of Alabama, for examination of *Hydroptila roberta*. This is Technical Contribution 2451 of the South Carolina Agricultural Experiment Station.

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**MICRODONOPHAGUS, A NEW ENTEDONTINE GENUS
(HYMENOPTERA: EULOPHIDAE) FROM PANAMA**

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Abstract.—*Microdonophagus woodleyi* Schauff (Hymenoptera: Eulophidae) new genus, new species, is described and illustrated. This species is a gregarious endoparasitoid of larvae in the genus *Microdon* (Syrphidae). The relationship of *Microdonophagus* to other genera of entedontine eulophids is discussed. Females of this species are fully winged but the males are brachypterous and are generally very different in appearance from the females.

In August, 1978, Norman E. Woodley collected a series of larvae of the genus *Microdon* Meigen (Diptera: Syrphidae) on Barro Colorado Island in Panama. Five of these larvae eventually were found to have been parasitized by a gregarious endoparasitic eulophid. Since there were no records of any parasites of these flies, I was asked to attempt to identify them. My study has revealed that the parasites belong to an undescribed genus of entedontine eulophid. Since their biological association may prove to be of interest, I have taken this opportunity to describe the species.

The larvae of species in the genus *Microdon* are known to be predators or scavengers in ant colonies. Outwardly they resemble slugs, and at least one species was described as a mollusc. Larvae of the *Microdon* species, which is apparently undescribed (F. C. Thompson, personal communication), were taken from the nest of *Tapinoma fulvum* Wheeler (Hymenoptera: Formicidae).

Morphological and sculptural terminology follows Graham (1959) and Harris (1979) respectively.

***Microdonophagus* Schauff, NEW GENUS**

Type species.—*Microdonophagus woodleyi* Schauff, new species.

Diagnosis.—Subfamily Entedontinae (sensu Peck et al., 1964 and Graham, 1959; tribe Entedontini sensu Burks, 1979); scutellum with 1 pair of setae; submarginal vein with 2 setae; funicle with 3 articles, club with 2 and terminal spine (Fig. 10); propodeum with single longitudinal carina (Fig. 5); posterior mesepimeron enlarged between coxae and meeting ventrally (Fig. 3); gaster petiolate; stigmal vein greatly reduced, sensillae arranged in a Y-shape (Fig. 9); postmarginal vein indistinct, only about as long as wide.

Description.—*Female*: Funicle with 3 articles, club with 2 plus terminal spine (Fig. 10); head (Fig. 2) broader than high, antennae inserted in middle of face,



Fig. 1. Habitus, *Microdonophagus woodleyi* male.

facial grooves lacking, dorsal occipital margin rounded, malar space more than $\frac{1}{2}$ eye height; pronotum with transverse anterodorsal carina, without posterior shiny margin; dorsal setae about $2\times$ as long as median width of pronotum; propleuron (Fig. 3) with anteroventral carina; prosternum trapezoidal, entire, perpendicular to lateral pronotum; mesoscutum (Fig. 4) with notauli indicated by sculptural change only, with posterior depressions; scutellum about as long as wide, gradually sloping, axillae not advanced cephalad of anterior margin of scutellum; metanotum a narrow band, expanded medially and slightly overhanging anterior propodeal margin; prepectus triangular in side view; division of mesepisternum and dorsal half of mesepimeron indistinct; posterior mesepimeron (Fig. 3) clearly set off by oblique suture, expanded between midcoxae and anterior

margin of metasternum and meeting medially; metapleural protuberance without carinae; mesosternum normally developed; propodeum with single median longitudinal carina, spiracular area sunken; forewing (Fig. 9) with stigmal vein greatly reduced, sensilla arranged in Y; postmarginal vein only about as long as wide.

Discussion.—When describing a genus with only a single included species, the question of what constitutes the synapomorphies of that genus is complicated by the inability to compare character states with other congeneric species. In my description of this genus I have relied on characters which are known to be reasonably stable in related genera of Entedontinae.

I regard the following characters as putative synapomorphies with a high probability of being shared by other species in *Microdonophagus*: 1) greatly reduced stigmal vein with sensillae arranged in a Y. Other entedontine genera which I have examined have stigmal veins which, although they may be short, are as long as or longer than wide. The group of four sensillae on the stigma are near the end of the vein, usually on a small swelling, and are arranged in a straight line. In addition, most closely related genera have a distinct postmarginal vein (usually longer than the stigmal). In *Microdonophagus*, the postmarginal is very much reduced and is nearly invisible under normal lighting and can only be distinguished with a phase contrast microscope. 2) posterior mesepimeron enlarged and meeting ventrally between the mid and hindcoxae. No other genus of entedontine has posterior sections of the mesepimerons that meet ventrally. In others, the posterior edge of that sclerite wraps only slightly around past the midcoxae and the ventral surface of the propodeum separates the two. In *Edovum* (Grissell, 1981), the posterior half of the mesepimeron is somewhat swollen and extends slightly ventrally. However, it remains widely separated by the mesosternum and ventral propodeum. 3) propodeum with single longitudinal carina. The other closely related genera all have different patterns of propodeal carinae and sculpturing which remain quite stable within the genera. 4) prosterna expanded with antero-ventral carina. Some species of related genera have the prosterna slightly swollen, but none have an expanded flange-like carina (Fig. 3).

This genus is closely related to *Edovum*, *Entedon*, *Horismenus*, and *Pediobius*. Females of these genera all have heavily sclerotized bodies, the dorsal thorax covered by distinct alveolate sculpture, an enlarged first gastral tergum, a distinct transverse carina on the pronotum, and carinae on both sides of the propodeal spiracle and a change in sculpturing. *Microdonophagus* can be separated from all the above genera by the four characters mentioned above. The states present in related taxa are: stigmal vein sensilla arranged in a row (stigmal vein usually developed); posterior mesepimeron not swollen and meeting beneath propodeum; propodeal carina variable (only *Entedon* with a single median carina and that is bordered laterally by a sunken area), prosternum not expanded and flange-like anteroventrally.

The aberrant morphology of the males of the type species makes it difficult to assess them in relation to other genera. The males of this species show some similarities to those of some species of *Mellitobia* and *Tachinobia repanda* (Bouček, 1977) which also have swollen femora, scapes, and reduced eyes and shortened funicular articles. However, the females of these groups are placed in Tetrastichinae and are not closely related to *Microdonophagus*. Until other species are collected, it is impossible to determine whether any of the unusual character states

found in the males is of generic significance. Here, I have assumed that other males of this genus may not share these states and have described the male only at the species level.

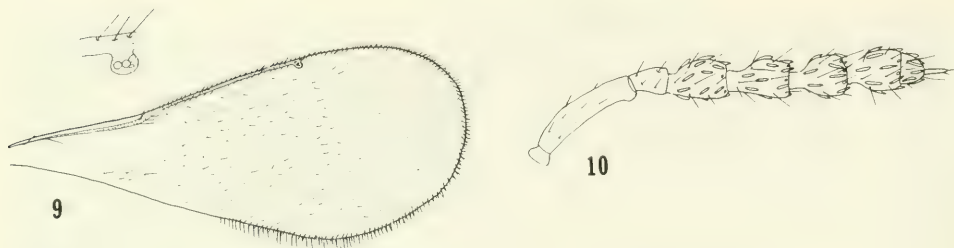
Microdonophagus woodleyi Schauff, NEW SPECIES

Holotype female.—Length 1.6 mm; color as follows: head, thorax, gaster black; pedicel, funicular articles, club, coxae, and 4th tarsomere brown; scape, rest of legs yellowish brown. Head (Fig. 3) alveolate, fading slightly above toruli and becoming smooth below and between toruli; width: height 55:37; eye height: malar space 23:16, inner ocular margins parallel; raised inverted V-shaped ridge between toruli; genal carina running from edge of oral cavity to level of midpoint of eye; malar suture absent; ocelli in equilateral triangle, OOL:POL 7:14; occiput rounded; mandibles bidentate, denticles subequal; antennae as in Fig. 10; thorax (including propodeum) evenly reticulate except posterior half of mesepimeron, area around metapleural protuberance, and propodeum laterad of median carina smooth; mesoscutum length: width 25:45, midlobe and each lateral lobe with 2 pairs of setae; scutellum length: width 28:38; propodeum length: width 10:30, with a number of small alveolae at each side of median carina, sculpture fading to smooth laterally and below carina, with a small seta above each spiracle; metapleural protuberance smooth; petiole minutely alveolate, slightly longer than wide; gaster ovate, tergum 1 covering slightly more than $\frac{1}{2}$ length of gaster, with a row of small setae at lateral margins, smooth dorsally and laterally except for small anterolateral alutaceous area; other terga subequal in length, with faint alutaceous sculpture dorsally; forewing as in Fig. 9; hindwing $4\times$ as long as wide, rounded apically.

Male.—Length 1.4 mm. Color as follows: head, thorax, gaster, and coxae brown; petiole black; antennae, femora, tibiae, and fourth tarsomere light brown; first 3 tarsomeres on all legs yellowish. Head height: width 42:30, smooth except lightly alutaceous below and laterad of toruli; frons acutely angled below toruli, with several small setae over oral cavity, with raised bump between toruli; eyes reduced (Fig. 1); ocelli in equilateral triangle; OOL:POL 8:14; malar suture absent; antenna with scape greatly swollen, densely setose, ventral surface excised (Fig. 6), funicle with 3 articles; club with 2 plus terminal spine; thorax smooth except lightly alveolate-alutaceous on lateral margins of mesoscutum, axillae, metanotum, propodeum, anterodorsal mesepisternum, and mesosternum; pronotum rectangular in dorsal view, with antero-lateral carina; propleura swollen ventrally; mesoscutum $2.5\times$ as wide as long, notaulices faint but complete, midlobe with 3 pairs of setae; scutellum slightly wider than long, axillae not advanced cephalad of anterior margin of scutellum; metanotum expanded medially, slightly overhanging anterior propodeum; propodeum $2\times$ as broad as long, median carina visible only anteriorly, with pair of submedian setae; spiracular area slightly sunken, carinae inconspicuous, callus with 2 setae, and an additional seta dorsad of spiracle; prepectus triangular in side view, reduced ventrally to a narrow band; petiole slightly longer than wide; gaster longer than wide; first tergum equal to $\frac{1}{4}$ of total length, other terga subequal, fore and midcoxae globular, hindcoxae longer than wide; fore and midfemora globular, nearly as long as wide; hindfemora about $2\times$ as long as wide; fore and midtibiae swollen apically; hindtibiae nearly cylindrical; first 3 tarsomeres (Fig. 7) of fore and midleg wider than long, first and



Figs. 2–8. Scanning electron micrographs of *M. woodleyi*. 2, Female head. 3, Female thorax, lateral view. 4, Female thorax, dorsal view. 5, Female propodeum and petiole. 6, Male scape, ventral surface. 7, Male foretarsi. 8, Male scape, magnified.



Figs. 9-10. 9, Female forewing and stigmal vein (inset). 10, Female antenna.

second with spatulate setae, fourth as long as wide; hindtarsomeres longer than wide; wings reduced, forewing about as long as thorax, veins indistinct; hindwing about as long as scutellum and propodeum combined.

Types.—Holotype ♀ on point with data: Panama, Canal Zone, Barro Colorado Island, Aug. 12, 1978. N. E. Woodley collector. Ex. *Microdon* sp. Deposited in the National Museum of Natural History, Washington, D.C. Five ♂ and 40 ♀ paratypes with same data as holotype. Paratypes deposited in the Canadian National Collection and British Museum (Natural History).

Notes.—A single *Microdon* larva that was preserved in alcohol contains approximately 60–70 pupae (eyespot visible on many, but not all) of *Microdonophagus*. These pupae fill the entire inside of the larva. No accurate count of the numbers of individuals that emerged from the other larvae was obtained. Many of these specimens were still pupae which had not emerged. Only the 46 specimens noted under types were sufficiently developed or intact to be used for the description.

The ventral surface of the scape of the males of this species (Figs. 6, 8) is unlike anything I have observed in other chalcidoids. The excised area is divided into 5 separate compartments each approximately the same size as a respective antennal article (pedicel, funicles 1–3, and club). Each compartment is separated by a transverse sclerotized ridge. Inside each compartment there is a small mushroom shaped organ which also varies in size depending on the size of the compartment, buttressed on 3 or 4 sides by small ridges which radiate out from the “mushrooms” to the sides of the compartments. Each of these structures consists of an inner and outer ring. Under high magnification, there appear to be several pores arranged between the inner and outer rings. It is likely that these pores secrete a substance onto the tops of the structure which can then be applied to the segments of the male’s antenna. These substances may then be used either in courtship (as seems most likely) or they might function in the male’s interactions with ants. The morphology of the males strongly suggests that they do not leave the ant nest after emergence and they would almost certainly come into contact with the ants after they emerge.

Etymology.—This species is named in honor of the collector, Norman E. Woodley.

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thank Z. Bouček for his comments on generic limits and Deborah Leather Roney for the habitus drawing.

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A NEW SPECIES OF *TAENIAPTERA* FROM THE UNITED STATES
(DIPTERA: MICROPEZIDAE)

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Abstract.—*Taeniptera feei*, new species, is described from the southernmost part of Texas, and is compared with related Mexican species. A previously wholly unknown and highly specialized development of the male copulatory apparatus of this fly is also described.

While collecting insects along pathways in the Los Palamos Management Area at Brownsville, Texas in 1976, Frank D. Fee, of University Park, Pennsylvania, collected 11 specimens of a micropezid that proved to be undescribed. The species belongs to the Taenipterinae, a subfamily of largely tropical distribution. Only six species have been found within the borders of the continental United States, although southward therefrom more than 200 species have been listed (Steyskal, 1965, 1968). The most recently named and still valid species of this subfamily known to occur within the United States is *Grallipeza nebulosa* (Loew), described in 1866.

Little is known about the biology of the Micropezidae. Some have been reared from decaying vegetable matter and dung, but one species is known to attack ginger roots in the Orient and another has been found in Europe feeding on the contents of leguminous root nodules (Müller, 1957; Steyskal, 1964, 1968). No biological or ecological data are associated with the new species beyond the fact that it was collected close to the ground. Additional collecting by Mr. Fee at the same time of the year in 1984 did not yield further specimens, probably because much further growth of vegetation along the pathways did not permit sweeping with the net close to the ground.

The species runs best in available keys (Hennig, 1934-1936; Steyskal, in press) to *Taeniptera*, although the wing vein closing the basal cubital cell (anal cell) is slightly shorter than the free part of that vein ($Cu_2 + Al$). Hennig (1934) stated in his key to the genera of the Taenipterinae that all such intermediate cases were to be considered to belong in the part of the key led to by the character of long closing vein. The species is, on that basis, definitely a member of the *munda* group, one I treated after examination of types in the British Museum (Steyskal, 1967), describing three new species and presenting a key to the group as an extension to Hennig's (1934-1936) key to *Taeniptera*. The *munda* group is distinguished by the open cell R_5 of the wing, the reddish thorax, and the presence of only one pair of dorsocentral setae. *Taeniptera feei*, new species, may be recognized with the following revision of my 1967 key:

- F (E). Ocellar plate extending but little anterad of anterior ocellus, finely rugulose; vertical humps various, dull to shining.
- G (H). Thorax evenly reddish, without or with more traces of brown cross-bands; vertical humps polished, shining; subbasal and medial wing bands (Fig. 1) connected in discal cell; lower margin of face with narrow mesal darkening; subgenital plate of δ as in Fig. 4 *T. feei*, n. sp.
- H (G). Thorax with distinct brown anterad of furrow; vertical humps dull to subshining; subbasal and medial wingbands not connected.
- I (J). Forebasitarsus nearly wholly white; vertical humps well developed, dull, anteriorly with one or two rugae; lower facial margin with complete narrow black band; δ subgenital plate virtually straight-sided, denticles strong *T. grata* (Wulp)
- J (I). Forebasitarsus black at tip for distance equal to diameter; vertical humps low, subshining; δ subgenital plate strongly narrowed medially, inner denticles minute *T. wulpi* Steyskal

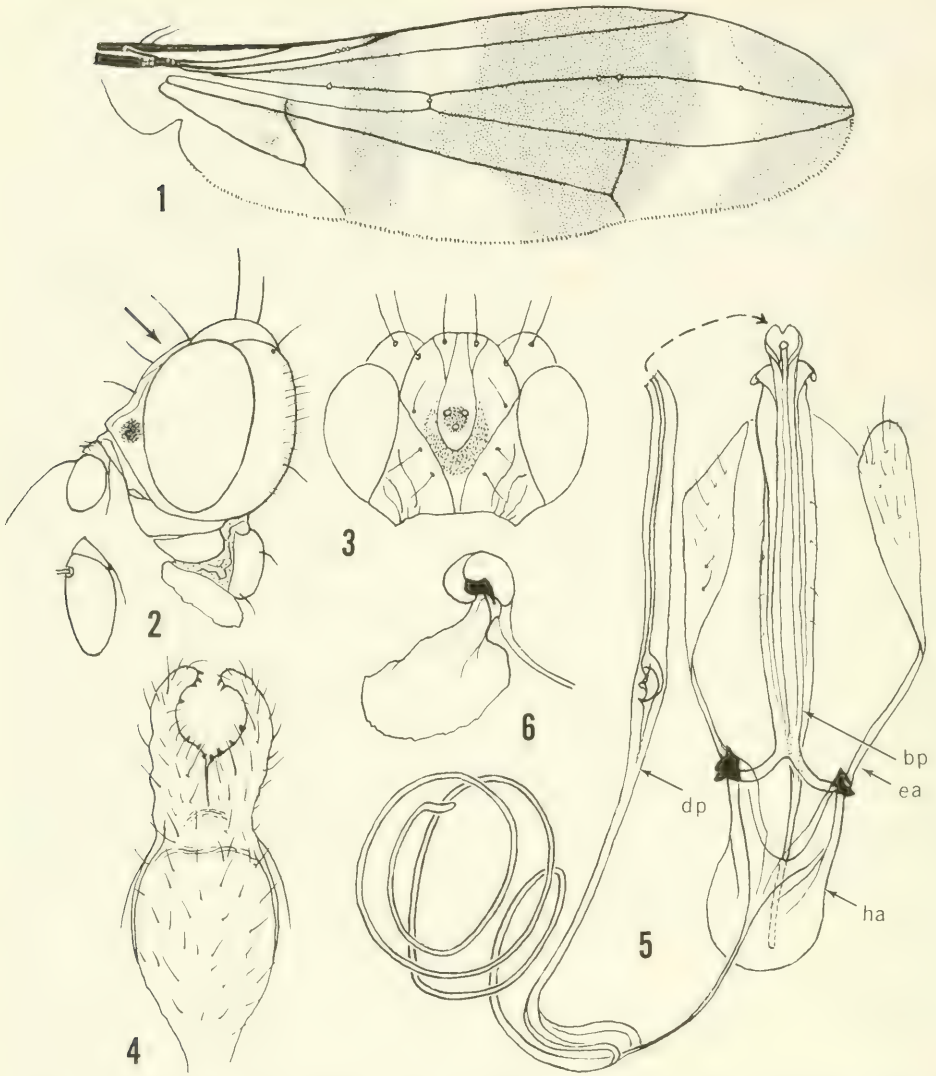
Taeniptera grata (Wulp) bears the greatest similarity to and is perhaps the closest relative to *T. feei*. Two species not in the revised part of the key, *T. munda* and *T. lauta*, differ considerably from the others in that they have the top of the head evenly rounded (lacking the posterodorsal humps) and wingvein Cu_2 (closing the basal cubital cell) considerably elongated. This leaves a rather well defined group which may be typified by *T. grata* (Wulp), of which *Mitromyia conifer* Cresson is a synonym. Should further investigation of the large and multifarious genus *Taeniptera* lead to means of defining and delimiting distinct genera, then *Mitromyia* may be found to deserve generic rank. The very apomorphic male genitalic structures described below are also found, with relatively slight differences, in *T. grata*, but lack of specimens for dissection does not permit a statement as to the structure of the male genitalia in other related species, nor what other structures may also occur within the present limits of *Taeniptera*.

Taeniptera feei, NEW SPECIES

Figs. 1–6

Length of wing in mm: δ 6.2–7.1 (average 6.3), η 6.37–6.92 (average 6.55).

Entire body reddish brown to brown, with following black markings: Head (Figs. 2 and 3) with roundish orbito-antennal spot, ocellar triangle, and small mesal spot on lower edge of face; thorax with narrow lower anepimeral (pteropleural) edge; abdomen with blotch (sometimes brown) on membrane below suture between 4th and 5th tergites and lesser blotch below tergite 3; eversible tip of ovipositor; of legs, foretibia, narrow tip of forebasitarsus, and all other tarsal segments (tip of hindtibia dark brown). Scutum with faint brownish crossband sometimes perceptible a little anterad of transverse furrow. Outer rim of thoracic calypter blackish. Legs with creamy whitish parts as follows: bands a little shorter than wide starting about $3.5 \times$ femoral diameter from tip of mid- and hindfemora; base (about $1.5 \times$ as long as wide) of midfemur; all basitarsi except tips (apical $\frac{1}{4}$ of fore-, apical $\frac{1}{4}$ of mid- and hindbasitarsi, delimitation rather indistinct). Parts of femora adjacent to whitish parts a little darker than remainder and base of midfemur a little paler. Halter with cream-colored stem and blackish knob. Nearly all bristles and hairs black; a few on fringe of alar calypter, all on basal abdominal syntergite, and row along inner edge of propleuron yellowish. Following areas



Figs. 1–6. *Taeniaiptera feei* Steyskal, n. sp. 1, Wing. 2, Head of male in profile, antenna in position of greatest expanse. 3, Same, dorsal view in direction of arrow in Fig. 2. 4, Fifth abdominal segment (copulatory fork), ventral view. 6, Andrium, ventral view of microslide preparation. bp—basiphallus, dp—distiphallus, ea—epandrium, ha—hypandrium.

conspicuously white microtomentose: face below interantennal ridge and above clypeus; orbit below orbito-antennal black spot along eye and upwards posteriorly to upper $\frac{1}{4}$ of postocular orbit, lower border of propleuron, mesal part of scutum from transverse furrow back to scutellum between dorsocentral setae; and most of lower part and posterior face of thorax below scutellum.

Head (Figs. 2 and 3): Upper, elevated, strongly convex parts and clypeus shining and smooth; interfrontal stripe tapering forwardly, narrow at foremargin; antennal bases separated by 0.24–0.37 (average 0.30) of distance between eyes at antennal level; distinct ridge extending between eyes; front above ridge slightly concave

and approximately at 90° angle to lower face; 3rd antennal segment in direct profile oval to elliptical, about twice as long as wide; arista bare at 80× magnification; small groups of short setulae at lower end of facial depression and similar hairs continued in row along lower margin to lowest point of gena; other setae as figured.

Thorax gently and evenly convex in profile; scutellum not upturned. Chaetotaxy: 2 ntpl, 1 pa, 1 pair apical sc; also with row of 10–12 stpl (sometimes much finer and shorter also close anterad of it and row of 5–6 smaller hairs just above hindcoxa and diverging forward from larger row. Wing as in Fig. 1, dark pattern consisting mostly of dark hairs, membrane only slightly darker. Sensilla on veins as marked with small circles on Fig. 1: 2 on Sc opposite basal end of cell bm, 6 on stem vein close basad of septum, 2 near tip of R_1 , 1 in middle of basal section of R_5 , 1 on crossvein ta, 2 near middle of large dark area on R_5 , and 1 on same vein in preapical hyaline area. Cell bcu (formerly termed anal) with distinct central dark spot; pale area about ta only slightly extending into discal cell. Legs: Length of foretarsal segments, starting with basitarsus, as 100:38:22:12:16; hindtibia with complete series of irregularly alternating antero- and posterodorsal proclinate setae little longer than half diameter of tibia, about 10 distinct among general setal vestiture.

Abdomen: Male (Figs. 4–6) with 5th sternite (copulatory fork) as in Fig. 4; andrium (Fig. 5) remarkably specialized; hypandrium (ha) U-shaped with broad anterior flange and extremely long, apically coiled filamentous extension from base of sinus entering abdominal cavity with extension from tip of aedeagus enveloping it; basiphallus (bp) with two curved branches at base joining antero-ventral corners of epandrium (ea) and extending backward to point where distiphallus (remainder of aedeagus, dp) is turned forward and finally envelops extension of hypandrium within body cavity; complex formation at considerable distance from base of distiphallus may include orifice of seminal duct; sperm pump (Fig. 6) with trilobate vesicle, broad asymmetrically expanded apodeme, and short efferent duct to base of basiphallus. Abdomen of female in preserved specimens with ovipositor sheath approximately 2.75 mm long; when totally everted, entire ovipositor 5 mm long, inversible portion black, composed of numerous close rows of minute, closely spaced spicules, no sharp distinction evident between sheath and inversible apical part; sheath at rest folded forward beneath abdomen, cuneate, gradually tapering to very slender tip.

Holotype ♂, allotype, and 1 ♂ and 1 ♀ paratypes, Texas, Cameron County, Brownsville, Los Palamos Management Area, 26.X.1976 (Frank D. Fee), in National Museum of Natural History, Washington, D.C.; 2 ♂ and 2 ♀ paratypes, same data, in Florida State Collection of Arthropods, Gainesville; 1 ♂ and 2 ♀ paratypes, same data, returned to Frank D. Fee.

Etymology.—The species name is a Latin genitive construction of the collector's name.

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REVIEW OF THE SAWFLY GENUS *LAGIUM*
(HYMENOPTERA: TENTHREDINIDAE)

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Abstract.—*Lagium* includes a single species, *L. atrovioleaceum* (Norton), which occurs in eastern North America. The color of the abdomen used to separate the two previously recognized species is found to be unreliable for species separation; therefore, *A. tardum* Norton is a **new synonym** of *atrovioleaceum*. Larvae feed on *Sambucus* and *Viburnum*. The genus is characterized, and the female ovipositor and male genitalia of *atrovioleaceum* are illustrated.

Lagium includes a single species, *L. atrovioleaceum* (Norton), which occurs in eastern North America. The larvae feed on the foliage of *Sambucus* and *Viburnum*. Konow (1904) described the genus and based it on the North American species, but he also included two species from eastern Asia. The Asian species, though very similar to the North American one, have since been placed in another genus, *Lagidina* Malaise (1945).

Rohwer (1912) was the first to study *Lagium* in detail. His study indicated the presence of six species, separated by "trivial characters, except in the males where the genitalia offer good differences." He distinguished them by color, slight differences in the shape of the female sheath, slight differences in the shape of the labrum, and differences in the shape of the harpe of the male genitalia. Even though Rohwer's illustrations show differences, the harpe is very thin, and when the specimen is dry, it may bend and dry in slightly different configurations thus appearing to be different. Also, Rohwer's illustrations appear to be at slightly different angles. Ross (1951) listed two species, separated by color, *L. tardum* (Norton) having a mostly orange abdomen and *L. atrovioleaceum* a black abdomen. After study of the female ovipositor, characteristics of the male genitalia, sculpturation of the body, sheath shape, and other features, I found no reliable differences on which species could be separated. All specimens have similar structural features. I could not distinguish consistent differences in sheath shape and labrum shape as Rohwer did. Although individuals may have either a red or black abdomen with no apparent intermediates, they are morphologically identical, and I consider them color forms of the same species.

***Lagium* Konow**

Lagium Konow, 1904: 246. Type species: *Allantus atrovioleaceus* Norton, by original designation.

The following will separate *Lagium* from other genera of North American Tenthredininae: Each mandible with 2 teeth; clypeus subtruncate to slightly circularly emarginated at center; eyes small, inner margins subparallel, far apart with lower interocular distance greater than eye length; malar space equal to diameter of front ocellus; occipital carina present, extending to top of head but absent behind postocellar area; antenna long, $2.4 \times$ head width, slender, setaceous, 1st segment longer than broad, 2nd segment about as long as broad, 3rd segment longer than 4th segment, segments 4 to apex decreasing gradually in length; tarsal claw with inner tooth subequal in width and length to outer tooth, not appressed to outer tooth, basal lobe absent; hindcoxa large, causing apex of hindfemur to nearly reach apex of abdomen; hindbasitarsus subequal in length to following segments combined; forewing with anal crossvein short, perpendicular, situated near base of wing, distal anal cell twice length of proximal anal cell; hindwing of female with anal cell petiolate, petiole about half width of cell at widest point, cells Rs and M present; hindwing of male with partial peripheral vein, absent only between radial cell and cell M; basal plates separated by a medial suture; cenchri small, far apart, nearly $3 \times$ farther apart than breadth of one.

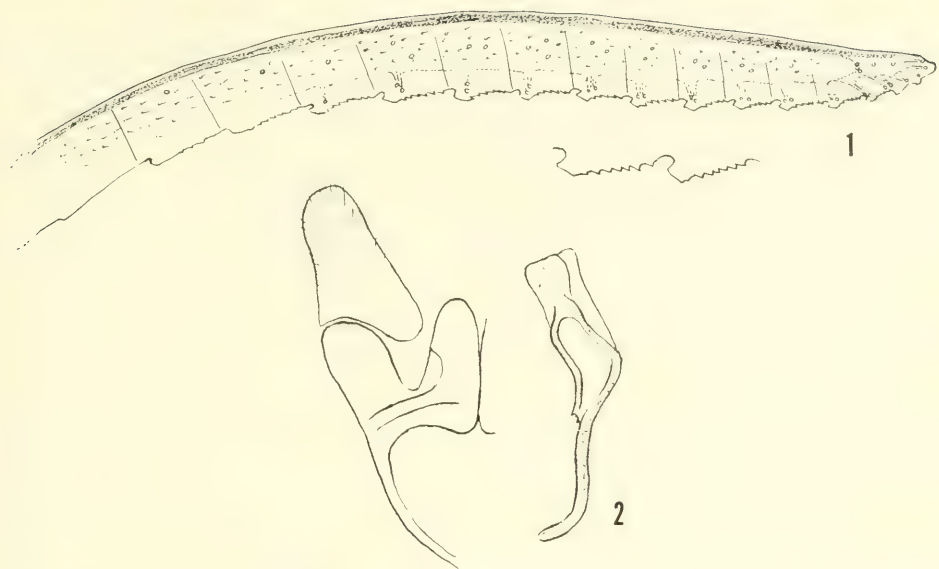
The most characteristic features are the long distal anal cell which is $2 \times$ the length of the proximal anal cell, the long inner tooth of the tarsal claw subequal in length to the outer tooth, small eyes with the lower interocular distance much longer than the eye length, bidentate mandibles, and subtruncate clypeus. The genera with which *Lagium* is most likely to be confused are *Leucopelmonus* (which has a smaller inner tooth than outer tooth on the tarsal claw and a deeply emarginated clypeus); *Aglaostigma* (which has the proximal anal cell of the forewing subequal in length to the distal anal cell and the anal crossvein at an angle); *Rhogogaster* (which has tridentate mandibles and a deeply emarginated clypeus), and *Macrophya* (which has quadridentate mandibles, extremely enlarged hindcoxae causing the apex of the hindfemur to exceed the length of the abdomen, and the eyes usually large with the lower interocular distance less than the eye length). *Lagium* may be separated by using Ross' 1937 key.

The Asian genus *Lagidina* contains about six species. Though sharing most characters with *Lagium*, they are distinguished by the compressed antennae, more strongly so in the males, and the complete peripheral vein in the hindwing of the males; in some the occipital carina is also present behind the postocellar area. Known hosts for the Asian species are *Glechoma* and *Viola* (Okutani, 1963). Okutani (1963) described the larvae of two Japanese species. They appear similar to the larva described by Dyar (1897) in being flattened and having thick papillae on the body, but it is difficult to compare the two descriptions.

Norton (1860) described the first two species belonging to *Lagium*, but later (1868) he regarded one, *tarda*, as only a color variety of the other, *atroviolaceum*. Dalla Torre (1894) placed this species in *Tenthredopsis* (a genus restricted to the Palearctic Region) following Provancher (1888). Rohwer (1912) treated six species of *Lagium* (including three new species), but only two were later listed by Ross (1951) and Smith (1979). Currently, only the following species is recognized.

***Lagium atrovioleaceum* (Norton)**

Tenthredo atrovioleaceus Harris, 1835: 583. Nomen nudum.
Tenthredo tarda Harris, 1835: 583. Nomen nudum.



Figs. 1–2. *Lagium atroviolaceum*. 1, Female lancet, with closeup of central serrulae. 2, Male genitalia, left half of genital capsule, ventral view, at left; lateral view of aedeagus at right.

Allantus atroviolaceus Norton, 1860: 255 (♀, ♂, described from Connecticut and Massachusetts; type ♀ in MCZ labeled “350 u” “Type #26299”).

Allantus tardus Norton, 1860: 246. (♀, ♂, described from 5 specimens from Connecticut, Massachusetts, and Maine; types not located). **NEW SYNONYMY.**

Tenthredo atroviolacea var. *peratra* Dyar, 1897: 192. (♂, larva; Franconia, New Hampshire; type in USNM).

Lagium angulabre Rohwer, 1912: 215 (♂, Baldwin, Kansas; type in USNM).

Lagium planifrons Rohwer, 1912: 216 (♀, ♂, from several Virginia localities; type ♀, E. Falls Church, Va., in USNM).

Lagium erythropus Rohwer, 1912: 214 (♀, Baldwin, Kansas; type in USNM).

Female.—Length, 13–16 mm. Black; apex of mandible dark reddish, labrum may be brownish; hindcoxa with white stripe on dorsolateral margin, not reaching apex of coxa; extreme apex of forefemur, outer surface of foretibia and foretarsus whitish; abdomen black or orange, the latter usually with orange on segments 2–6 and part of 7 but sometimes with sterna blackish. Wings uniformly, darkly, black infuscated; veins and stigma black. Sheath slender, of approximate uniform width in dorsal view, rounded at apex in lateral view. Lancet as in Fig. 1.

Male.—Length, 11–13 mm. Color similar to that of female; white line on hindcoxa may be absent, but same area usually somewhat paler than rest of coxa; outer surface of fore- and midfemora and outer surface of apical half of hindfemur may be dark orange in some specimens that have an orange abdomen. In specimens with orange abdomen, orange present on segments 2 to apex except for blackish apex of hypandrium. Genitalia as in Fig. 2.

Larva.—Known only from the description by Dyar (1897) who stated that it is a “very curious one.” “Looks a little flattened, but thick and robust. Feet on joints 6–13. Head round, dull black; width 1.4 mm. Body segments 7–annulate, the

whole body soft dark gray, the ground color uniform. A series of short thick papillae, one on each annulet in subdorsal and lateral even regular rows, and other smaller ones scattered subventrally. First row (subdorsal), which is the shorter, has the papilla on annulet 1 orange, 2–4 black, 5–6 orange, 7th black; second row (lateral) which is larger, has 1st to 4th orange, 5th to seventh black; two behind the spiracle and two subventrally posteriorly pale orange; two groups of six to eight very small ones on the upper and lower subventral folds whitish. Sides with a number of small black spots. On thorax there are less of the papillae, but the alternation in color is similar. Anal plate not differentiated.

Ultimate stage.—Smooth, very shiny, entirely dark slaty blue black, papillae indicated by very small concolorous points. Thoracic feet pale.”

Characteristic of the Tenthredininae are the 7-annulate segments. However, *Lagium* is difficult to distinguish from other genera since larvae of others have not been adequately defined. The flattened appearance and obvious papillae with alternating coloration may help in its recognition.

Distribution.—Eastern North America from New Brunswick to Georgia west to Ontario, Minnesota, Iowa, Kansas, Oklahoma, and Louisiana. I have seen specimens from the following states and provinces: District of Columbia, Connecticut, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Missouri, New Brunswick, New Hampshire, New Jersey, New York, North Carolina, Oklahoma, Ohio, Ontario, Pennsylvania, Quebec, Rhode Island, South Carolina, Tennessee, Virginia, West Virginia, Wisconsin.

Hosts.—Reared from larva on elder, *Sambucus* sp., by Dyar (1897). A specimen in the USNM was reared from *Viburnum* sp. at Middleboro, Massachusetts. Both hosts are in the Caprifoliaceae.

Ecology.—Dyar (1897) did not expand on the life history but stated that the larvae enter the earth to form a “moderately firm hibernating cell.” There is probably a single generation a year since adults have been collected only in spring and early summer. Flight periods range from April 21 to August 3 (earliest and latest records I have seen) with most in late May through June. In Canada they have been collected from May 20 to July 9; in the central Atlantic states from May 25 to July 6; and in the midwestern states from May 12 to July 15. In a Malaise trap situated in a stream bed with low mixed vegetation in Louisa Co., Va., 52 specimens were collected from May 25 to June 29, 1985; males were most common in the first half of the collecting period whereas females were most abundant in the latter part (Table 1). According to specimen labels, adults have been collected on *Ceanothus*, on *Ceanothus* flowers, on *Myrica cerifera*, and in vegetation along streambank. I have found them in sweepings of low vegetation in open deciduous forests near streams or rivers. Habitats of the host plants are the obvious places to look for this species.

Discussion.—The general habitus of this species, being a large sawfly, black or black with an orange abdomen, and with black wings, will help distinguish it from most other Tenthredininae.

I was unable to find differences in sheath or labrum shape or differences in the structure of the harpe of the male genitalia as was reported by Rohwer (1912). Based on identical morphological features, I regard both color forms to represent the same species even though I have not found evidence of intermediates in color except a few specimens of the red abdomen form that have a slight degree of

Table 1. Seasonal occurrence and numbers of specimens with a red and black abdomen collected in a single Malaise trap in Louisa Co., Va., 1985.

Collection Date	Black		Red		Total
	♀	♂	♀	♂	
May 25	0	2	0	1	3
June 1	1	5	0	2	8
June 9	3	12	5	0	20
June 15	5	2	5	0	12
June 29	3	1	5	0	9
Total	12	22	15	3	52

infuscation on the venter. Color alone cannot be considered a reliable character unless supported by morphological or biological differences, neither of which are evident.

In collections, specimens of the black form outnumber the red form 2.5:1 (approximately 460 specimens examined; 330 black, 130 red). In mapping the occurrence of the two color forms, there is an indication of a north-south cline, the black form more common in the north and the red form in the south. All specimens examined from New Brunswick, Maine, Quebec, the Ottawa area of Ontario, and Minnesota were black. Mixed collections are found from New Hampshire, southern Ontario, Michigan, and Wisconsin south to South Carolina and Kansas. The few specimens examined from Georgia, Oklahoma, and Louisiana were the red form. There was no indication of an east-west pattern. Of the 52 specimens collected in the trap in Louisa Co., Va., in 1985, 34 were black and 18 red. More red females than black females were caught, but there were 7 × more black males than red males (summary of collections in Table 1).

ACKNOWLEDGMENTS

The following individuals kindly allowed examination of specimens in their collections: Henri Goulet, Biosystematics Research Institute, Agriculture Canada, Ottawa; D. W. Webb, Illinois Natural History Survey, Champaign; Howard E. Evans, formerly at the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Roland L. Fischer, Michigan State University, East Lansing; Roy R. Snelling, Los Angeles County Museum of Natural History, California; Robert E. Lewis, Iowa State University, Ames; and Donald S. Chandler, University of New Hampshire, Durham. Other specimens are in the National Museum of Natural History, Washington, D.C. (USNM). I appreciate the help of Mr. and Mrs. J. G. Kloke, Louisa Co., Va., for their help in collection of specimens. Fig. 1 was prepared by my wife, J. L. Smith. I appreciate the suggestions of the following reviewers: W. W. Middlekauff, University of California, Berkeley; R. J. McGinley, Smithsonian Institution, Washington, D.C.; and J. P. Kramer and E. E. Grissell, Systematic Entomology Laboratory, USDA, Washington, D.C.

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A NEW *CHLAMYDASTIS* (OECOPHORIDAE, LEPIDOPTERA)
FROM TEXAS

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Abstract.—A new oecophorid moth, *Chlamydasitis habrolepis*, is described from specimens collected in extreme southern Texas. The adult male, denuded male wings, eighth abdominal segment of male, and male and female genitalia are figured. This represents the first species in this genus known to occur in the U.S.A.

This new species of *Chlamydasitis* is known from a series of 24 specimens collected by the authors at two localities in extreme southern Texas. *Chlamydasitis* is a large genus including about 65 species, nearly all of which were described by Edward Meyrick. The genus is widely distributed in Central and South America, and one species, *C. dominicae* Duckworth, was described from the island of Dominica in the West Indies. Up to now, no species in this genus has been reported to occur in the U.S.A. As is the case in other genera in the subfamily Stenomatinae, the male genitalia are characterized by the presence of specialized scales, strongly attached to the inner margin of the valve. In the case of *Chlamydasitis*, these scales are usually conspicuously dilated at their apices, forming an arrowhead shape. This is not a reliable generic character, however, as it is absent in some species and found occasionally in other stenomatine genera.

Chlamydasitis habrolepis Blanchard & Knudson, NEW SPECIES

Figs. 1-6

Description.—*Head:* Front and vertex white; labial palpus ascending to just above front, 2nd segment white, flecked with blackish brown, 3rd segment white with blackish rings at base and just before apex. Male antenna yellowish white with numerous setae, which are from 2-3 times the length of segments; female antenna very shortly setose. Collar white. *Thorax:* White with blackish scales at tips of tegula and mesonotum. Foretibia white with longitudinal black stripe along inner margin; terminal segments of tarsus black; midtibia and tarsus white with 5 or 6 transverse black stripes along outer surface; hindtibia and tarsus mainly whitish. *Abdomen:* Shiny yellowish gray. *Forewing:* Upper surface white, lightly sprinkled with brownish scales. Extreme base from costal margin to fold blackish brown. Along costal margin beyond, are three additional blackish brown spots; at $\frac{1}{4}$ the distance from base, just beyond middle, and $\frac{1}{4}$ the distance from apex, the last always being the largest. On the middorsal margin is a large blackish brown blotch, which extends slightly above fold and is often divided longitudinally by an oblique white stripe. Small intense black discal spots are found at the middle

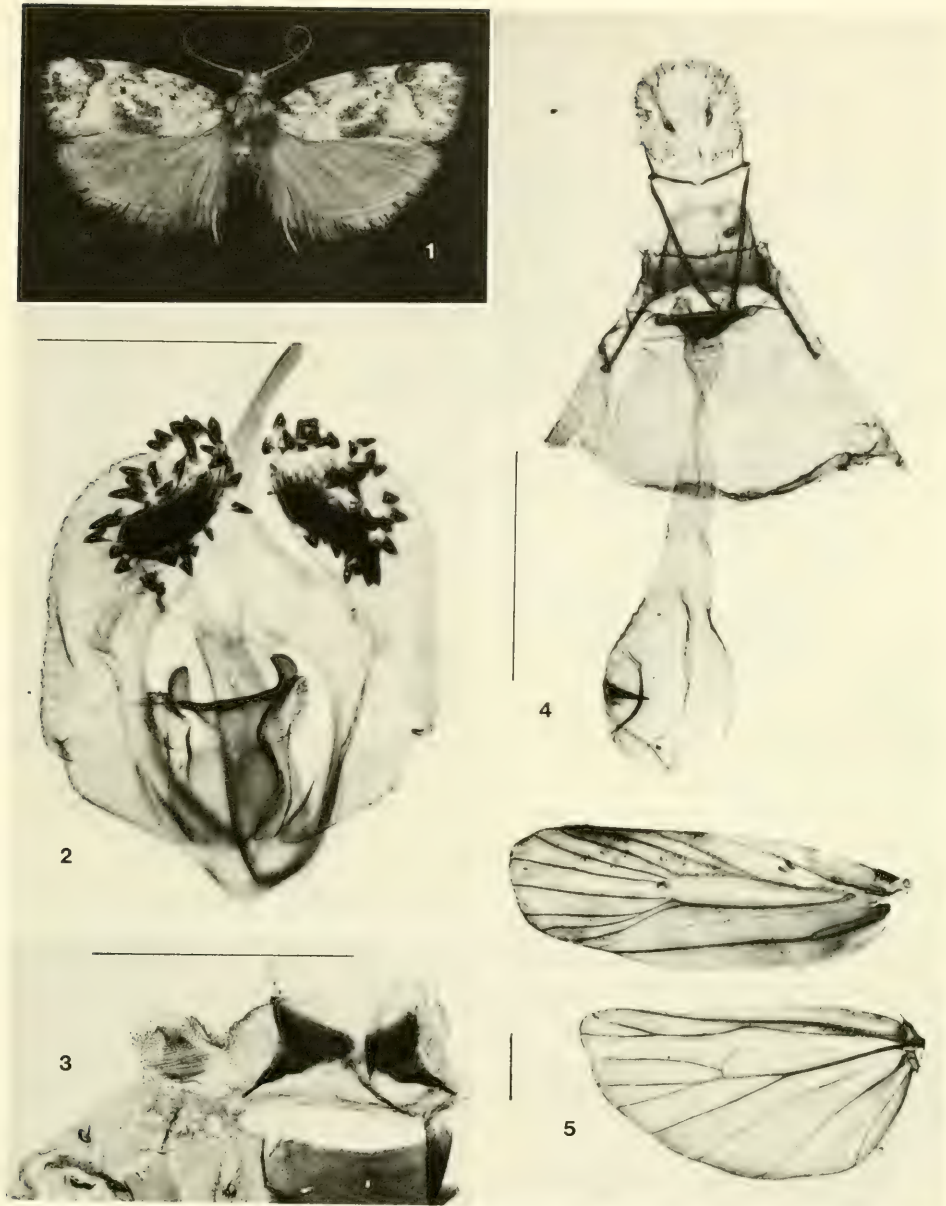
and apex of cell, the latter surmounted by a short black dash. Bordering the inner margin of the subapical costal spot and extending obliquely to tornus, is a thin black line; beyond this line is a variably sized blackish brown blotch over the middle of the subterminal space, often joined to the lower margin of the subapical costal spot. Fringe blackish brown, often checkered with white. Under surface dark fuscous, apical $\frac{2}{3}$ of costal margin yellowish white. *Hindwing*: Pale fuscous with a dark terminal line and a second dark line in fringe. *Length of forewing*: Males, $n = 21$, 5.4–7.4 mm, average 6.1 mm. Females, $n = 2$, 6.8 and 6.9 mm. *Wing venation* (Fig. 5): Forewing with 11 veins; 4 radials; M2 connate with the stalk of M3 and Cu1, from the lower outer angle of cell; 1A obsolete. Hindwing with 8 veins; discocellular incomplete; 1A normal. *Male genitalia* (Figs. 2, 3, 6): Fig. 2 represents male genitalia with aedeagus in situ, from slide AB 4570; Fig. 6 is a drawing made from slide AB 1183, representing the male genitalia on the left, and frontal and lateral views of aedeagus on lower right and tips of specialized scales on valvae at upper right; Fig. 3 represents the eighth abdominal segment of a male, sternite on right, from slide ECK 1187. *Female genitalia* (Fig. 4): Frontal view from slide AB 5398. Papillae anales membranous, moderately setose; apophyses posteriores $1\frac{1}{2}$ times the length of apophyses anteriores, both slightly clubbed apically. Apophyses anteriores continue caudally as a sclerotized ridge along lateral margin of 8th tergite. Ostium bursae a well sclerotized, broad funnel, leading to a membranous ductus bursae, which widens gradually to corpus bursae. Signum a well sclerotized spined keel.

Types.—Holotype (Figs. 1, 2): ♂, Cameron Co., Texas, Laguna Atascosa, 1-IV-78, collected by A. & M. E. Blanchard and deposited in the National Museum of Natural History. Paratypes: Same locality as holotype, 24-IV-73, 10 ♂ (one with genitalia on slide AB 5400); 25-IX-73, 1 ♂ (genitalia on slide AB 5399); Hidalgo Co., Texas, Santa Ana National Wildlife Refuge, 20-IX-66, 1 ♂ (genitalia on slide AB 1183); 15-IX-74, 8 ♂ (one with genitalia on slide AB 4669), 2 ♀ (genitalia on slides AB 4670 and AB 5398), all collected by A. & M. E. Blanchard and deposited in the National Museum of Natural History. Santa Ana National Wildlife Refuge, 5-IV-80, 1 ♂ (genitalia on slide ECK 1181), collected by E. C. Knudson and retained by collector.

Remarks.—In the genus *Chlamydastis*, as it now stands, the maculation of adults varies considerably, although many species have a pattern similar to *C. habrolepis*. However, the combination of the oblique, black subterminal line and well marked black middorsal patch on the forewing of *habrolepis* is not present on any of the 62 species of which we have seen illustrations (Clarke, 1955; Duckworth, 1969). The male genitalia of the new species are similar, but hardly identical to those of *C. bifida* (Meyrick), *forcipata* (Meyrick), *ptilopa* (Meyrick), and *tritropa* (Meyrick). We have seen few examples of female genitalia of other *Chlamydastis* sps., but of the 9 species illustrated by Clarke (1955), 6 appear to show the extension of the apophyses anteriores described above.

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The authors are extremely grateful to W. Donald Duckworth, who examined the first specimen collected by the senior author and has reviewed our manuscript.



Figs. 1-5. *Chlamydastis habrolepis*. 1, Holotype. 2, Genitalia of holotype, slide AB 4570. 3, 8th abdominal segment of male paratype, slide ECK 1187, Santa Ana Refuge, 5-IV-80. 4, Female genitalia of paratype, slide AB 5398, Santa Ana Refuge, 15-IX-74. 5, Left wings of male paratype, slide AB 5399, Laguna Atascosa, 25-IX-73. Line segment in Fig. 2 represents 0.5 mm; in Figs. 3, 4, 5, 1 mm.

We thank him especially for giving us permission to depict the beautiful drawing by George Venable in Fig. 6. We also thank Ronald W. Hodges for his assistance. Finally, we wish to acknowledge the assistance and cooperation of officials of the Laguna Atascosa and Santa Ana National Wildlife Refuges.

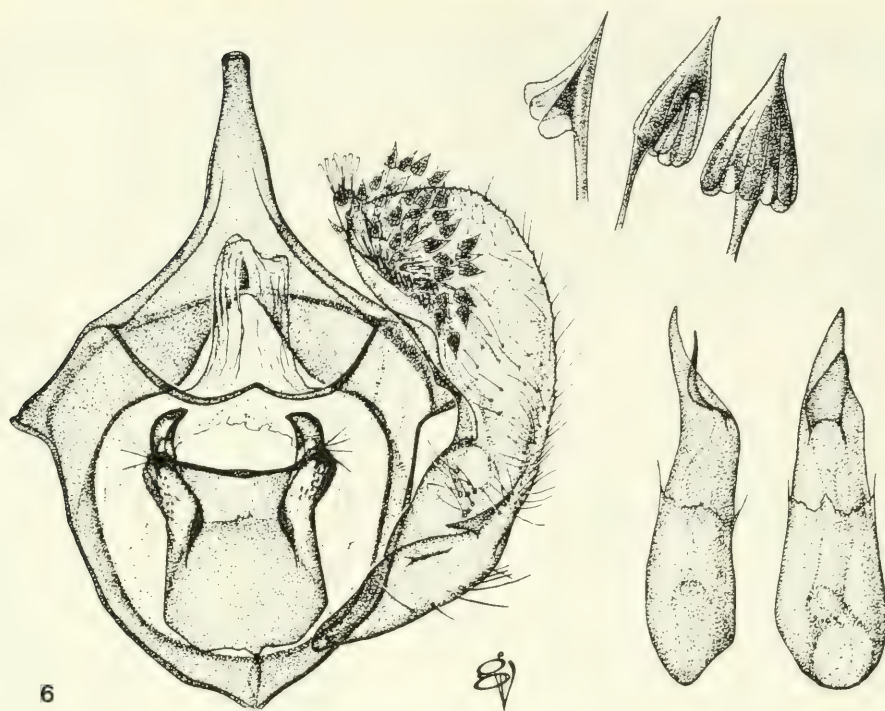


Fig. 6. *Chlamydastis habrolepis*, male genitalia, aedeagus, and specialized scales, from slide AB 1183, Santa Ana Refuge, 20-XI-66.

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NOTE

Liriomyza trifolii (Burgess) (Diptera: Agromyzidae) Overwinters
Outdoors in Maryland

The leafminer *Liriomyza trifolii* (Burgess) is a serious pest of numerous horticultural crops grown in fields and greenhouses. Although prevalent in southern United States, the insect's distribution also includes the District of Columbia, Delaware, Pennsylvania, New Jersey, Iowa, and Ontario (Spencer, 1973. *The Agromyzidae (Diptera) of Economic Importance*. Dr. W. Junk, The Hague). Whether this occurrence in northern states and a Canadian province is the result of greenhouse collections, summer outdoor collection of insects that have escaped from greenhouses, or collections of truly overwintering field populations is unclear.

In order to determine if the insect, which usually pupates just beneath the soil surface, could overwinter in Maryland, we placed four wood frame cages (50 × 40 × 35 cm) covered with fine mesh screening (leafminer adult-proof) in a heavily infested field of dahlias located in Kingsville, Maryland (14 km NE of Baltimore) on 23/X/84. Cages had open bottoms and were sunk 5–10 cm into the soil next to an infested plant. Each cage had a tightly fitted removable screen lid. Several dahlia leaves with larva-filled mines were placed in each cage at set-up, as were two yellow sticky boards (Olson Products, Media, OH). The boards were replaced 17 times through the fall, winter, and spring. A maximum/minimum thermometer was placed in one cage, and at each visit, the maximum and minimum temperatures were recorded.

The dahlias were killed by frost on 8/XI/84. From frost until 9/I/85, 217 adults were captured on the yellow boards. From 9/I/85 until 11/IV/85 no miners were caught. Between 11/IV/85 and 25/IV/85, 11 *L. trifolii* adults (2 males, 9 females) were caught (at least 2 adults/cage). No adults were found on boards on subsequent visits. All of the spring-collected adults were deposited in the insect collection of the National Museum of Natural History. The lowest recorded air temperature in the monitored cage was –26°C (between 9/I/85 and 1/II/85). High temperatures (37°C maximum) may have triggered adult emergence in April.

We conclude that *L. trifolii* is able to overwinter in Maryland. The results indicate that greenhouse infestations in the spring may be attributable in part to adults moving inside from either infested outdoor fields or from infested leaf litter removed to outdoors from the greenhouse. The results also suggest that a few of the insects diapause, we suspect as pupae. The number of adults captured after frost totaled 228 of which 11 overwintered. This suggests that a relatively low percentage (4.8%) of the leafminers that tolerated cold conditions actually overwintered.

We thank George Steyskal for identifying the overwintered insects and Henry Fischer for letting us use his field of dahlias. The project was in part supported by the Fred C. Gloeckner Foundation, Incorporated. Mention of a product does not constitute an endorsement by the authors or their employers.

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NOTE

Records of *Eriotremex formosanus* (Matsumura), *Sirex edwardsii* Brullé,
and *Neurotoma fasciata* (Norton) in Louisiana
(Hymenoptera: Siricidae, Pamphiliidae)

Eriotremex formosanus (Matsumura), an Asian horntail, was first collected in North America in Chatham County, Georgia, in November 1974 (1975 USDA Coop. Econ. Ins. Rpt. 25: 899). Smith (ibid.: 851–854) reported its occurrence in three counties in Alabama, compared it with our native *Tremex columba* (L.), discussed its habits, and provided a key to the genera of North American Siricidae. This species has also been found in several counties in Florida (ibid.: 899; 1976 USDA Coop. Plant Pest Rpt. 1: 112, 239, and 865; 1977, 2: 873) and in Charleston, South Carolina (ibid., 1980, 5: 629). The first Louisiana specimens were collected in September, 1979, by R. E. Clary at his home in East Baton Rouge Parish. They emerged from the upper part of the trunk and lower branches of a hickory tree which had been cut down in the summer of 1978 because it was dying. The identification was confirmed by D. R. Smith, Systematic Entomology Laboratory, USDA. Three other specimens from this parish, collected on October 13, 1981 and September 21 and October 9, 1983, were found in collections of students in beginning entomology courses, although the label data may be incorrect. One specimen was found in a rain barrel 2 miles NW of Norwood, Section 67, in East Feliciana Parish by A. D. Oliver on September 25, 1983, and another was observed at the same location four days later.

A single specimen of *Sirex edwardsii* Brullé, labeled Gueydan, Vermilion Parish, LA, 4-XI-1978, B. F. Turner, pine tree, represents a new state record for this species, previously known in the south from Alabama, Georgia, and Arkansas (Smith, 1979, *In* Krombein et al., Cat. Hym. in America North of Mexico, Smithsonian Institution Press, Vol. 1: 3–137). D. R. Smith made the identification.

Smith (1979, ibid.) reported that the distribution of *Neurotoma fasciata* (Norton) extended from Quebec to Florida and west to Wisconsin and Missouri, and (personal communication), that it had been found in Georgia. In a summary of insect conditions in the United States for 1965 (1966 USDA Coop. Econ. Ins. Rpt. 16: 158), this species was reported damaging peaches in Texas. This is an error as the original report in 1965 (ibid., 1965, 15: 734) referred to *N. inconspicua* (Norton).

Larvae of *N. fasciata* were collected for the first time in Baton Rouge on black cherry, *Prunus serotina* Ehrh., on May 30, 1979, by A. D. Oliver. He also observed this species infesting a black cherry tree near Atmore in Escambia County, Alabama, although no specimens were collected. L. D. Newsom collected it from black cherry in June, 1979, near Woodville in Wilkinson County, Mississippi.

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NOTE

Apobaetis etowah (Traver), A New Combination in
Nearctic Baetidae (Ephemeroptera)

Apobaetis was established by Day (1955. Pan-Pac. Entomol. 31: 121–137) for the aberrant Californian species *A. indepressus* Day, described from larvae and reared adults. Other than the specimens from California, *Apobaetis* has been known only from larvae from Kansas (Leichti, P. M. 1982. Tech. Publ. State Biol. Surv., Kans. 12: 13–16), which we cannot yet differentiate from those of *A. indepressus*. Although Day's rationale for erecting *Apobaetis* relied on the distinctiveness of larvae, there were adult characters that clearly separated it from other baetids, including the species of *Pseudocloeon* Klapálek known to Day. These characters included: 1) turbinate eyes of the male with nearly contiguous bases posteriorly and widely divergent bases anteriorly, 2) a prominent penes cover between the bases of the male genital forceps, and 3) an elongated basal segment of the male forceps. Traver (1935. In Needham, J. G., J. R. Traver, and Y. C. Hsu. The Biology of mayflies. Comstock Publ. Co., Ithaca, NY. 759 pp.) had earlier described *Pseudocloeon etowah* Traver from adults collected from the Etowah River vicinity of Georgia. She referred to its uniqueness among other species assigned to *Pseudocloeon*, specifically noting the distinctive male genitalia (illustrated 1935: Fig. 168). Traver's reference to the turbinate eyes as, "far apart at the anterior margins, closely approximated at the rear.," and the reported form of the basal segment of the forceps are also suggestive of *Apobaetis* characteristics.

We recently compared the type material of *A. indepressus* and *P. etowah*. Comparisons of the above characters, wing venation (see Fig. 18 in Day, 1955), egg morphology (extracted from one paratype subimago female of each species exuviating to the adult stage), and external thoracic and head morphology, confirmed our suspicions about the generic placement of Traver's species, and we therefore transfer *Pseudocloeon etowah* to *Apobaetis*, giving the **New Combination**, *Apobaetis etowah* (Traver).

Adult males of *Apobaetis* species are differentiated by the prominent and truncate margin superposing the penes cover in *A. etowah* (see Fig. 168 in Needham, Traver, and Hsu, 1935) and the much less prominent margin superposing and following the contour of the penes cover in *A. indepressus* (see Fig. 359 in Edmunds, G. F., Jr., S. L. Jensen, and L. Berner. 1976. Mayflies of North and Central America. Minnesota Univ. Press, 330 pp.). The larva of *A. etowah* remains unknown.

We thank W. J. Pulawski, California Academy of Sciences, San Francisco; Q. D. Wheeler, Cornell University, Ithaca; and J. E. H. Martin, Biosystematics Research Institute, Ottawa, for the loan of type material, and P. Leichti, State Biological Survey of Kansas, Lawrence, for loan of material. This paper has been assigned Purdue Experiment Station Journal No. 10,415.

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NOTE

New Combination and New Synonymy in North American
Stenopodius (Coleoptera: Chrysomelidae: Hispinae)
with a Taxonomic Note on Uroplatini

While revising the nearctic species of *Brachycoryna* (Coleoptera: Chrysomelidae: Hispinae) I found that *Brachycoryna lateralis* Schaeffer (1933, Pan Pac. Entomol. 9: 105) belonged in the genus *Stenopodius*. *Stenopodius* is the only nearctic genus in the tribe Uroplatini in which the third tarsal segment is not bilobed. *Stenopodius lateralis* also differs from other species of *Brachycoryna* by having eight rows of punctures on each elytron instead of ten.

Further investigation revealed that *S. lateralis* is conspecific with *S. vanduzeei* Blaisdell (1939, Trans. Am. Entomol. Soc. 64: 440). Couplet A in Blaisdell's (1939: 427) key concerns the shape of the anterior pronotal margin. *Stenopodius lateralis* keys out at this couplet. *Stenopodius vanduzeei* differs from all other species of *Stenopodius* by having the anterior margin of the pronotum straight and having eight rows of punctures on each elytron. Comparing the types, I was unable to find a single non-sexual character to separate the specimens.

The lectotype of *S. lateralis*, here designated (Ft. Collin[s] Colo[rado], Schaeffer Collection, H. S. Barber Bequest, 1950, U.S. National Museum) is a male while the holotype of *S. vanduzeei* is a female.

The previously recorded range of *S. lateralis* is Colorado and California. I have also seen specimens from Arizona (Gila Bend), Minnesota (state label only), and Wyoming (state label only).

Stenopodius lateralis differs from all other species of *Stenopodius* by having the anterior margin of the pronotum straight rather than angularly produced at middle. This necessitates a change in Arnett's (1973, Beetles of the United States) key XIV on page 916. Couplet nine should be changed to read:

- 9(8). Third tarsal segment obviously bilobed *Brachycoryna*
– Third tarsal segment not bilobed *Stenopodius*

The life history and biology of the species of *Stenopodius* are unknown. In the National Museum of Natural History in Washington, D.C. there is a series of *S. lateralis* from Arizona, Gila Bend, 26/VI/48, H. S. Barber, host plant-*Sphaeralcea emoryi* J. Torr. (Malvaceae). These specimens were taken in a mixed population with *S. texanus* Schaeffer. There are two larvae on points with this collection, so one of the species was breeding in *Sphaeralcea*. Further collecting is needed to clarify this situation.

I thank N. D. Penny (California Academy of Sciences) and R. E. White (Systematic Entomology Laboratory, Agricultural Research Service, USDA) for allowing me to examine specimens in the collections under their care. R. E. White also commented on an earlier draft of this manuscript.

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BOOK REVIEW

Aphid Ecology, by A. F. G. Dixon. Blackie & Son Limited, Glasgow and London, distributed in the U.S.A. by Chapman and Hall, in association with Methuen, Inc., 733 Third Avenue, New York, NY 10017. 157 pp. 1985. \$39.95/cloth.

Dr. Dixon's book, *Aphid Ecology*, is an excellent review of the ecology of aphids—those small, usually soft-bodied, sap-sucking, rapidly reproducing insects that are often serious pests of agricultural crops, ornamental plantings, and forest trees.

In 1973, Dr. Dixon wrote *Biology of Aphids* (The Institute of Biology's Studies in Biology No. 44, 58 pp.), and *Aphid Ecology* is a logical expansion of the information included in the former publication—with the notable omission of any information on aphids as virus vectors, which is itself a book-length topic.

Aphid Ecology contains 10 chapters: An introduction (identification and classification information), host selection, size in aphids, polymorphism, cyclical parthenogenesis, life-history patterns, dispersal, population dynamics, community structure and species diversity, and an epilogue. There is also a list of the scientific (and some common) names of the aphids referred to in the text. The scientific names are repeated in the index so that it is very easy to find them in the text.

Dr. Dixon has spent more than 20 years studying the intricacies of aphid populations. Despite his own personal depth of knowledge on the subjects covered, Dr. Dixon validates his statements and examples through references to more than 380 publications—a bibliography of wide and varied use in and of itself. While the usual, long-studied aphid topics of host selection, polymorphism, parthenogenesis, host alternation, and dispersal are brought up-to-date, a reader's fascination with the world of aphids is enhanced by discussions of some of the newer attributes of aphids such as a discussion of the discovery of the 'soldier' morphs in *Colophina* spp. and 'biters' in *Astegopteryx styracicola* Takahashi. We can but wait until the next intriguing event in an aphid life cycle is discovered!

The book is well illustrated with good line drawings and charts. The few scanning electron photomicrographs and photographs of slide-mounted specimens seem to be unnecessarily dark, but they do convey the intended messages. Both the binding and the paper should stand a lot of handling. While the author says that his book "... is written for specialists, postgraduates, and advanced undergraduates in entomology," I would also recommend it to generalists and amateurs with interests in natural history and to everyone interested in the fascinating world of aphids. I fear that the price of \$39.95 will discourage some prospective buyers.

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BOOK REVIEW

Chironomidae of the Holarctic region. Keys and diagnoses. Vol. 1. Larvae, edited by Torgny Wiederholm. Entomologica Scandinavica Supplement 19. 455 pp. 1983. \$73. *A catalogue of the chironomid genera and subgenera of the world including synonyms (Diptera: Chironomidae)*, by Patrick Ashe. Entomologica Scandinavica Supplement 17. 68 pp. 1983. \$15. *A review of the genera Doithrix n. gen., Georthocladius Strenzke, Parachaetocladius Wülker and Pseudorthocladius Goetghebuer (Diptera: Chironomidae, Orthocladiinae)*, by Ole A. Saether and James E. Sublette. Entomologica Scandinavica Supplement 20. 100 pp. \$19. 1983.

The Chironomidae are a group of aquatic insects long shunned by many aquatic biologists, and with good reason. Ubiquitous, incredibly abundant and numerous in genera and species, their identification, even at the generic level, has long posed a considerable problem. The works reviewed here go a long way towards solving that problem.

Chironomids have long been considered key elements in any aquatic fauna, but, in general, their identification and taxonomy have been so difficult that the group is often listed only at the family level in many studies. Although a number of identification keys have appeared, these suffer from a lack of information, illustrations, incorrect taxonomy and misdeterminations. The *Chironomidae of the Holarctic region* provides the necessary information that benthic biologists have long been seeking.

The book is hardbound and printed on high quality paper. It is arranged in 12 chapters, with two introductory chapters, and two final chapters devoted to references and an index. Eight of the ten subfamilies of Chironomidae are represented in the Holarctic region; each is provided with its own chapter. The list of authors of the chapters reads like a "Who's Who" of chironomid specialists: Brundin, Cranston, Fittkau, Oliver, Pinder, Reiss, Roback and Saether.

Too often, benthic biologists rely solely on dichotomous keys for identification of organisms, or perhaps just a picture that "matches." In this volume, we have the best combination—keys, illustrations, and most importantly, diagnoses. With a group as complicated as the Chironomidae, keying to a genus in a key is insufficient. It is far too easy to make a mistake and land in the wrong place! A diagnosis should always be consulted, and those offered in this volume are concise and often contain crucial information needed for separating similar genera. Each genus also has its own page (or pages for more complex genera) of clear illustrations of important generic characters. Keys to subgenera or species groups are offered for some genera. Comments are also given on distribution and general ecology for each genus.

This volume belongs on the shelf of every aquatic entomologist and/or benthic biologist involved in faunal surveys or identification work. However, it can not be considered a panacea for their identification woes. The keys are for fourth instar larvae; earlier instars may differ. Not all genera are known in the larval stage (described genera with unknown larvae are listed in each chapter). The keys often utilize structures which can only be observed in correctly prepared specimens

under high magnification. The book is not an easy tool for the uninitiated in chironomid morphology to use. Explanation of morphological terms used in the keys is limited to three pages of explanatory plates in the second chapter. It is recommended that the novice worker obtain a copy of Saether's *Glossary of chironomid morphology terminology* (Entomologica Scandinavica Supplement 14, 1980, \$13.60) to use with the holarctic keys. Many of the characters used in the keys, such as the frontal apotome, will be new to North American workers. The keys themselves work fairly well. The Tanypodinae key seems ponderous, but does enable one to finally separate the genera of the *Thienemannimyia* group. The key for the Chironominae works extremely well.

The volume suffers only in some minor aspects. First, it appears to me that very few people are aware of its existence. Many state environmental personnel and consulting biologists I have been in contact with did not know of it. Sales of the first volume in the United States have been rather low according to information I've received from the various authors of the text and the editors. This may be due to overzealous xeroxing, probably as a result of the high price of the volume. *Entomologica Scandinavica* is fast becoming the journal for chironomid systematics papers, but cannot continue to publish such papers if copies are not sold because of the reluctance of some workers to purchase them. This volume is but the first of a proposed three volume set dealing with the larvae, pupae and imagines. The complete set was (and may still be) available at a substantial discount if one purchased all three volumes together. (The second volume, covering pupae, will soon be published.)

Typographical errors are minor and few. The most noticeable occurs on page 383, where *holoprasinus* is misspelled *holoprasinatus*. The one mistake I could find was in the Chironominae chapter. In figure 10.62, the authors illustrate the mentum and antenna of *Polypedilum* (*Polypedilum*) *tuberculum* Maschwitz. However, since the species is described in Maschwitz's unpublished Ph.D. thesis, the authors have created a nomen nudum. "Publication" of a xeroxed copy of a thesis by University Microfilms does not constitute publication according to the International Code of Zoological Nomenclature. The new (1985) Code makes this position relatively clear in regards to theses and dissertations.

The second work, Ashe's *Catalogue of chironomid genera*, is a godsend for chironomid taxonomists. In this paper, Ashe lists all known chironomid genera, a total of 524, of which 355 are considered valid. Valid genera are listed in boldface type; their synonyms, nomina dubia and nomina nuda in lighter type. Also included are the authors' name(s), date, type-species and comments concerning the taxonomy of the genus if necessary. A special section at the end of the paper deals with fossil genera, most of which are considered incertae sedis. A perusal of this listing of 23 generic names makes it clear that much remains to be done with the taxonomy of fossil chironomids.

Ashe has done an incredible amount of work in producing this paper; he has seen all of the literature involved and has consulted with experts on various genera. Anyone who does not make chironomid taxonomy a specialty knows what a nightmare it is to trace a given name; it is exasperating and time-consuming to one already equipped with a well-stocked library of chironomid literature. Eminently clear, concise and readable, this catalogue stands out as a model for catalogues for other families. No chironomid systematist should be without it.

The third paper reviewed deals with a monophyletic group within the subfamily Orthocladiinae. It is a paper done in the typical Saether style, well illustrated (by Saether's wife, Unni), and covering adult males and females, pupae and larvae when possible. Sublette's influence is seen in the number of scanning electron micrographs presented. Modern chironomid taxonomy demands that characters from all life stages be used to delimit taxa whenever possible. Characters from one life stage are not sufficient to unravel complex relationships between genera or groups of genera. This paper utilizes all the taxonomic information available.

Most of the chironomids covered in this paper are apparently semi-terrestrial or found in seeps, small springs, etc. Much of the material utilized by the authors was collected by an extremely adept and dedicated collector, Pat Hudson. Hudson's collecting efforts in areas not heavily collected for chironomids have gone a long way towards advancing the state of chironomid systematics.

We have here three excellent papers dealing with chironomid systematics, all published by a journal which is becoming a major voice in that field (and we need one). The first two are a must for anyone dealing with chironomids in general, the third more for specialists. I would encourage workers to purchase the entire three volume set of the *Chironomidae of the Holarctic region*. These publications can be ordered from Scandinavian Entomology Ltd., P.O. Box 24, S-240 17 S. Sandby, Sweden (include \$2.75 for postage for each item ordered). The discount for ordering all three volumes of the Holarctic keys may still be in effect. You will be acquiring a state of the art series of monographs which are destined to become classics.

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BOOK REVIEW

Aphids on the World's Crops, An Identification Guide, by R. L. Blackman and V. F. Eastop. John Wiley & Sons, Baffins Lane, Chichester, Sussex PO10 1UD, England. 466 pp. 1984. \$60.00/cloth.

It is not easy, especially for non-specialists, to make quick and accurate identifications of insects; and identifications of aphids have been particularly difficult. The specificity of some aphid species to particular plant species is well established and can be useful information when working with and identifying aphids. In order for the aphid-plant relationship to have predictive value, two important, restrictive facts must be established: (1) the aphids must be *colonizing* (feeding and producing young) a particular plant and (2) the plant must be identified correctly. On page 1, the authors state this proviso as being essential to the use of their keys. And indeed, everyone must follow these two conditions because the characters used in the keys could fit several aphid species, but only the one that colonizes the host treated.

The book contains seven sections. Section A (pages 1-27) contains general information on systematics, life cycles, developmental morphs, and morphological characters used in the identification of aphids. Section B (pages 29-208) begins with another warning on the limitations of the keys and a summary of procedures for their use. A list of both the Latin and common names of the crops treated is followed by an alphabetical listing of crops, each with a list of the aphid species most likely to be found colonizing the crop and then a key to those particular aphid species. Three short keys to commonly-encountered, polyphagous aphids complete the section.

Section C (pages 209-373) is devoted to a systematic review on the aphid species treated in the keys. Information on the appearance in life, habits, biological development, etc. is given and selected references are cited. Section D (pages 375-377) is a brief statement on collecting, preserving, and slide-mounting aphids. Section E (pages 379-384) refers the reader to publications dealing with the myriad of topics associated with aphids, e.g. faunal works, general biology, morphology, anatomy, physiology, genetics, migration and dispersal, host-plant relationships, bibliographies, and relationships with other insects. Section F (pages 385-413) lists the references cited, and Section G (pages 415-466) is a series of photographs of slide-mounted examples of the aphids covered in the text.

This publication brings together information available previously only in widely-distributed, individual papers containing species descriptions and keys. By using the information in the keys, in the systematic reviews, and in the photographs, a non-specialist should be able to identify, with a good degree of accuracy, pests colonizing any of the horticultural or agricultural crops treated.

It is unfortunate, but understandable, that the authors did not include keys to alates of the species treated. But omission, for the most part, of information on alates will prevent the misuse of such information by workers trying to identify alates collected in traps. The format makes specific information easy to find, but it necessitates a lot of turning from one section to another in order to check an identification.

The book is hard-bound and is printed on good paper. The line drawings are good; and, while the photographs are often too light and the morphological characters in them small, they do illustrate most of the characters mentioned in the text. A few species were omitted under some of the crops, but apparently the demand for this book has been such that a second edition is forthcoming, and it will contain additions and corrections.

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BOOK REVIEW

The Biology of the Muscidae of the World, by Peter Skidmore. Dr. W. Junk Publishers, Dordrecht, The Netherlands. For USA and Canada: Kluwer Academic Publishers, 190 Old Derby St., Hingham, MA 02043. [i-xii &] 550 pp. \$165.00.

This book gives an excellent overview and synthesis of the biology of a large, diverse, and fascinating family of flies. The book also, and this is not reflected in the title, describes in a comprehensive manner the eggs, larvae, and puparia for most of the approximately 450 muscids for which those stages are known. Many immatures are described here for the first time. We think of muscids as the great dung feeders and barnyard pests, and they are, but the larvae of many are predators, plant feeders, or bird parasitoids. In fact most muscids are obligate carnivores and hatch as second or third instars. Immature stages are known for only about 12 percent of the 3600 described muscids. Since a good cross section of the family is represented in this sample, there is adequate basis for the generalizations made in this book.

Chapters or sections are unnumbered. The first 42 pages summarize the biology and introduce the reader to the study of the immature stages. This section discusses the history of studies on muscid immature forms, the morphology and terminology of these stages, and predictions that can be made about the biology of various kinds of muscids on the basis of their anatomy. It follows with tips on preparation, examination, and identification of immatures, proposes a revised higher classification of Muscidae based on all life stages with particular emphasis on immature stages, and gives a synopsis of a newly proposed classification. Except perhaps in the Coenosiniinae, larval characters appear to be more conservative than adult characters and so show affinities more clearly than do adults. This section ends with keys to larvae by subfamily, tribe, genus, and species. The keys are only partial, of course, and it is still not possible to characterize many genera as entities in a key.

The bulk of the book is entitled, "Survey of the Biology of World Muscidae." The survey has an orderly and consistent plan. The subfamilies and their nested tribes, genera, and species are treated similarly: first a description of the egg, larva, and puparia, followed by paragraphs on biology, affinities (any adult characters discussed are under this section), and distribution. Treated this way, similar data for various taxa are easy to find and compare. Plates of figures usually directly follow descriptions of species, a particularly convenient feature. Most species are illustrated with excellent, detailed drawings. Specimens are sometimes drawn from various aspects and some species are illustrated with more than one example of a particular stage to show variation. Most drawings are original; the few that are not are redrawn with attribution. A few adult drawings show unnamed species so that they may be identified later. Page 356, figure 108a-d, shows an undetermined *Spilogona* sp., but it is referred to as 108i-j in the text. This and two or three typographical misspellings of scientific names in the text, never in headings, were the only errors I noticed.

The book ends with a list of references, apparently completely covering the

primary literature of the immature forms, and a taxonomic index. A glossary would have been useful for such terms as eurytopic and stercoricolous. New terms here, I think, are mono-, di-, and trimorphic, describing whether a species has one, two, or three instars after leaving the egg. There is a convenient one-page list for the meanings of abbreviations used in the figures and text.

Skidmore depended on others for his nomenclature, and I suspect those who helped him in this regard expected to publish some taxonomic changes before this book appeared. A few new names for common taxa are used here and may cause a little confusion until the explanation for the changes is published. Thus *Gymnodia* is treated as *Brontaea* and *Brontaea quadristigma* (Thomson) is indicated as the name to use for *Gymnodia arcuata*, but we don't know who made or will make the synonymy and why. Citations are not given for generic or specific names, so a user without access to much of the literature may have difficulty finding the reason for the change. In any case, better to have the book sooner than later. When in a few years all the name changes will have been validated, the book will be right up to date.

Anyone who needs to identify the immature stages of Muscidae or know more detailed information about their biology than is available in general textbooks should have this book. It should remain a standard reference and continue to serve for many years. The volume is well bound and printed on good quality paper.

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THE LIFE OF A CALIFORNIAN POPULATION OF THE
FACULTATIVE MILKWEED BUG, *LYGAEUS KALMII*
(HETEROPTERA: LYGAEIDAE)

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Abstract. — *Lygaeus kalmii* is bivoltine in Monterey County, California. A major portion of the spring generation develops at sites distant from milkweeds; these nymphs feed on insect carrion as well as the seeds of *Lepidium nitidum* (Cruciferae) and other forbs. Cohorts reared in the absence of milkweeds survive well and produce viable offspring. The adults of the spring generation undertake dispersal flights during the late morning and afternoon on sunny days. Following dispersal, these adults are closely associated with *Asclepias eriocarpa*, a host that they can apparently locate by using olfactory cues. Milkweed seeds do not become available until several weeks after the spring adults disperse; the bugs do not copulate during the first part of this interval. The large populations of adults that move to *A. eriocarpa* during June and July can do considerable damage to the plants. These voracious adults also scavenge the numerous insects that are trapped in the milkweed pollinia, cannibalize each other, and, interestingly, attack the pupae of the monarch butterfly, *Danaus plexippus*, and the egg masses of the milkweed beetle, *Chrysochus cobaltinus*. The second generation feeds heavily on milkweed seeds. The reduviid, *Rhynocoris ventralis*, is a predator of adult *L. kalmii*.

Lygaeus kalmii Stål is a conspicuous bug that is commonly encountered in stands of milkweeds (*Asclepias* spp.) throughout much of North America (Slater and Knop, 1969). Our knowledge of this species has accumulated in a manner that is considered exemplary by scientific philosophers. Following the early descriptive work by Townsend (1887) and Simanton and Andre (1936) on life history, research has focused on the detailed, more carefully controlled examination of particular aspects of the biology, e.g. Caldwell's (1974) work on dispersal behavior and Evans' (1983) studies of the factors influencing host selection. Simultaneously, observers have amended and corrected the original descriptions as new details came to light (e.g. Dingle and Caldwell, 1971; Price and Willson, 1979). During this process, the species has been shown to display considerable geographic variation in morphology (Slater and Knop, 1969) and recent reports (Hunt, 1979; Slater, 1983; Wheeler, 1983) demonstrate that host requirements are less restricted than previously assumed. Data from collections and the literature lead one to suspect that there is interesting regional variation in phenology, food habits, and dispersal behavior. Our understanding of *L. kalmii* has thus reached a stage where it is useful to examine the life of a local population on the basis of these new insights.

My aim in this paper is to describe the niche of *L. kalmii* in Monterey County, California, and to report field observations on aspects of its biology that have been studied chiefly in the laboratory. To provide an account that is coherent, yet brief, I will comment on published results from other populations only in those cases where the comparison or verification is of particular interest. Readers seeking a complete bibliography on this species can consult Slater (1964, 1983), Evans (1983), and Wheeler (1983).

ENVIRONMENT

My observations focused on a *Lygaeus kalmii* population that inhabited a large tract of land (ca. 500 ha) at the Hastings Natural History Reservation in the Coast Range, Monterey County, California. This locality has mild, wet winters and hot, dry summers; conditions during my major period of study (Fig. 1) were normal for the region. The vegetation on the study area (490–820 m elevation) forms a complex mosaic of broadleaf evergreen forest (moist slopes), chaparral (dry slopes), and deciduous oak woodlands (Griffin, 1974).

All of the *Lygaeus* I found were in open woodlands and long-abandoned hayfields that had been established by merely removing a few trees from oak "savannas" (White, 1966). The herbaceous layer in these habitats is dominated by annual grasses and forbs that set seed and dry in late spring. *Asclepias eriocarpa* Benth., the only prevalent milkweed on the study area, occurs in these same, open habitats. These plants were distributed in 19 isolated stands that contained from 10–200 ramets. In addition, there was a large stand, which I will refer to as the "Arnold Field," of several hundred ramets scattered over an area of ca. 8 ha. Based on the recollections of residents and old notes, it is likely that many of these stands are at least 40 years old and that some may be much older. *Asclepias eriocarpa* is a large perennial that remains succulent throughout the summer.

PROCEDURES

I studied the populations at the Hastings Reservation in 1975 (17 April–21 July, 20–23 October), 1976 (11–19 August), and 1983 (1–4 August). My general approach was that of a naturalist. I went out almost daily to observe and take notes in the field; these activities served to continuously raise and refine questions that were answered by further observations and simple experiments. Similar observations made on *Lygaeus* species in Colombia, Colorado, Missouri, and New York helped me to place this Californian population in perspective.

The adults in two milkweed stands, as well as some of the bugs that were observed in experimental cages, were given individual marks by placing tiny dabs of rapid-drying enamel on the pronotum and corium. Marked bugs were observed to fly at least 30 m and to survive at least 21 days in the field.

The densities of *L. kalmii* and other arthropods on milkweeds were measured as follows. While walking along a predetermined direction across a milkweed stand, I stopped every seventh stride and, with my eyes closed, pointed to a spot to my right and about 3 m away. The milkweed stem growing most closely to this spot was circled slowly and all of the large, active insects were counted. A beating sheet was then placed beside the stem, which was cut at its base and searched carefully. All of the insects on the stem (or surrogates for any that were observed to escape) were placed in a vial of ethanol. The ground around the base

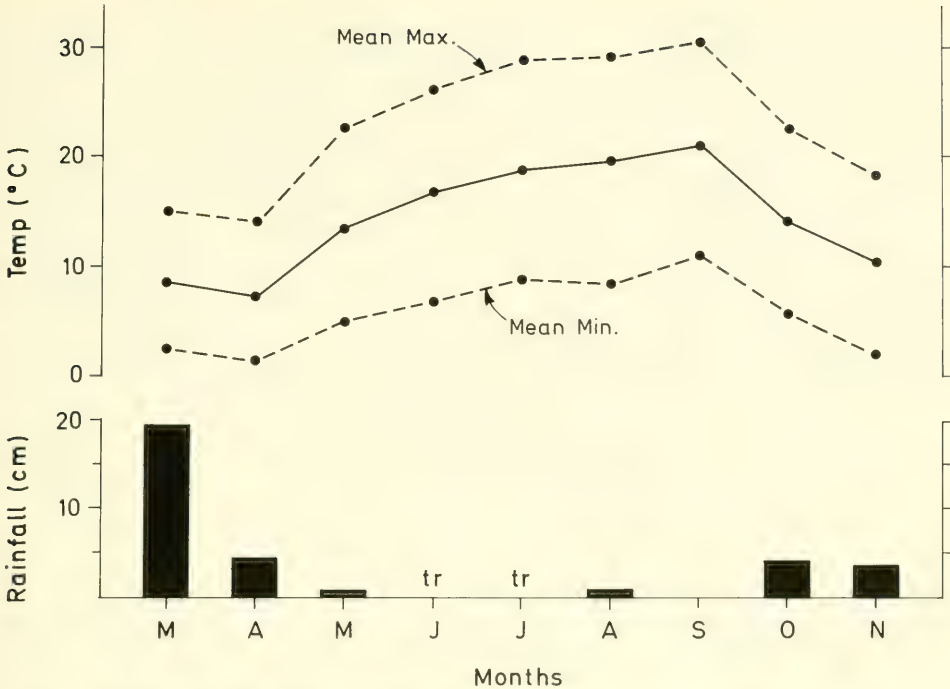


Fig. 1. Weather conditions at the Hastings Reservation during 1975. The weather station is located near the lower end of the study area at 545 m elevation. The extreme temperatures during this year were -7°C in January and 41°C in July. "tr" indicates a trace of precipitation.

of the stem was next searched for insects known to feed commonly on milkweeds. The aboveground plant parts were separated into foliage, inflorescences, pods, and stems; these were later dried and weighed. Each sample consisted of at least 50 stems collected in this manner.

I employed a variety of special censuses and simple experiments to examine particular aspects of behavior. These will be described with the results.

Field results were supplemented by observations on bugs reared in petri plates and assorted small jars. All cages had large openings, covered by dacron mesh, for ventilation. The bugs always had access to water which they obtained by probing absorbent cotton in vials that were filled with spring water. The cages were kept outdoors in a location where they were under light shade from mid-morning to late afternoon. The bugs were transferred to a clean cage about every 10 days. Since rearing conditions were uncontrolled, I did not measure developmental rate, clutch size, or other population parameters that were likely to depend on temperature and humidity.

I identified all of the insect species mentioned in the text. Voucher specimens, labelled "Lot 1120," have been placed in the Cornell University Insect Collection. James R. Griffin checked all of the plant identifications.

SEASONAL CYCLE AND HABITAT USE

Adult *L. kalmii* have been found overwintering in woodrat houses at the Hastings Reservation (Linsdale and Tevis, 1951). When my observations began in

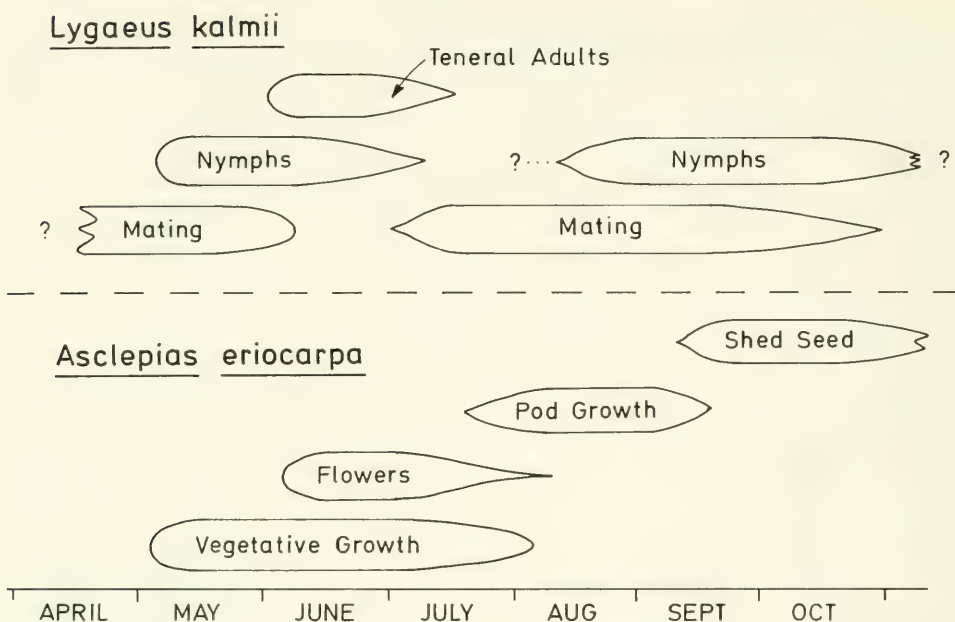


Fig. 2. Approximate phenology of *Lygaeus kalmii* and *Asclepias eriocarpa* at the Hastings Reservation, Monterey County, California. ? indicates occurrences that were inferred rather than directly observed.

mid-April, adults were already foraging in the open and copulating. The species is thus active well before the green shoots of milkweeds, *Asclepias eriocarpa*, poke above ground in early May (Fig. 2). Small aggregations, containing nearly equal proportions of both sexes, were found at this season near dried milkweed stalks that were produced the previous year. No milkweed seeds were found on the ground in most of these stands even though I made a concerted search for them. Furthermore, several aggregations occurred at locations at least 100 m from a milkweed stand. On 9–12 May 1975, I marked the bugs that had gathered within a 5 m² area, away from milkweeds, along a dirt lane. The density varied from 15 to 25 adults during this period. Three males remained on the area for at least four days. Since the sex ratio of newly marked bugs was about equal and males were recaptured more frequently (6 of 7 recaptures on 12 May and 5 of 5 on 14 May), it seems likely that the females tend to leave such aggregations relatively quickly.

During April and May the bugs were localized in open areas where individuals could easily move between patches of bare soil and herbaceous cover. Diggings by fossorial mammals and the edges of dirt roadways often provided these conditions. At this season the bugs foraged and mated chiefly on the ground. When it was cool and sunny, they spent much of the time running about where the sun had warmed the soil; when the ground was hot and after sunset, they tended to retreat to sheltered locations such as down cracks in the soil or under the basal rosettes of forbs.

I observed a female lay a large, but sterile, clutch of eggs in the field on 21 April. The earliest viable clutches, however, were not found until 12 May. The oviposition sites I discovered in the field included the hollow stems of dried forbs,

the crevices between the appressed, terminal leaves of milkweeds, and the exposed surface of a fallen leaf. In the cages, females oviposited in the hollow stems of forbs (the diameter of the cavity had to be large enough that they could insert the terminal portion of the abdomen), in wads of absorbent cotton, and under excised leaves.

On 15 and 16 May, I located several groups of first and second instar nymphs. Some nymphs were present in the milkweed stands, but the bulk of this new spring generation was located in favorable sites away from milkweeds. These sites presented a mosaic of bare soil and herbaceous vegetation and usually contained an assortment of weedy forbs. While such areas are often associated with disturbance, they nonetheless form a large portion of the natural, ungrazed grassland at the Hastings Reservation because of the extensive activities of pocket gophers, *Thomomys bottae*. I studied young nymphs by marching across the grassland, throwing down a tarpaulin as I approached a likely looking area, and then carefully searching around its edges. I frequently encountered densities of 5^+ nymphs/m² at locations over 40 m from the nearest milkweed. Early instars were usually discovered under basal rosettes of forbs or moving along the ground in spots where sparse vegetation provided partial shade.

During May, the intact carcasses of dead adults were frequently encountered in the milkweed stands and on the margins of bare patches in the open grassland. Some of the overwintered generation of adults persisted, and continued to copulate, until mid-June.

Development of the nymphs proceeded rapidly during May and the first teneral adults appeared during the first week of June. At this time, the annual plants that dominate the herbaceous vegetation were becoming quite dry; the milkweeds, however, were succulent and just beginning to bloom. It seems clear that the spring generation can complete development well away from milkweeds. For instance, on 14 June I found late instar nymphs at seven of nine sites that were located in grassland at least 30 m from the nearest milkweed stem (I had not searched previously for bugs at these stations). On this date, I swept fifth instar nymphs from the grass at three other locations over 150 m from the nearest milkweed. Older nymphs were present in milkweed stands but their densities appeared to be comparable with those encountered in the open grassland. Almost all of the spring generation had completed development by 19 July.

Following dispersal (described below), the new generation of adults was closely associated with milkweeds. These adults spent much time up on plants where they fed heavily on flowers and buds. Between 15 June and 3 July, no copulation was seen among the thousands of adults that I encountered. Less than 0.1% of a huge population that I observed on 4 July were mating. In mid-July, when copulating pairs were regularly seen, the succulent milkweeds in the most vigorous stands were just beginning to initiate pods. All of the plants in the less vigorous stands began to yellow at this time; several stands that were heavily used by *L. kalmii* in June and early July did not produce any seed pods during either 1975 or 1976.

My knowledge of *L. kalmii* at the Hastings Reservation during the remainder of the year is based on my observations in October 1975 and August 1976 and 1983, and by notes made, at my request, by John Davis, James R. Griffin, and Walter Koenig. Despite the onset of copulation in July, we were unable to find

nymphs of the summer generation until 17 August when a few scattered first and second instars were found on milkweeds. At this time, the plants had pods that were nearly mature size, but none of these had opened yet.

In late summer, adults continued to copulate and forage on milkweeds and on the ground nearby. Adults were often found below ground, in the spaces between the milkweed stalks growing from the same root crown and in recent diggings by pocket gophers. While a few adults continued to lurk around the dried out milkweed stands, the bulk of the population was concentrated in vigorous stands with maturing pods. No adults or nymphs were found away from milkweeds in the types of habitats that were used so extensively in the spring.

Milkweed pods began to open in mid-September; the shedding of new seeds continued through October. In late October 1976, after the onset of the autumn frosts and rains, adults and nymphs (including some in the second instar) were still concentrated in the vigorous milkweed stands where they often foraged on the ground. A few adults were copulating in late October. W. Koenig (personal communication) found active nymphs and adults out as late as 20 November and 12 December 1976, respectively.

FOOD HABITS

The appearance of adults before milkweeds emerge and the occurrence of both nymphs and adults at great distances from milkweeds indicate that *L. kalmii* can reproduce and develop by using other resources. To determine what these alternative foods might be, I carefully observed (often with a 4× magnifier) feeding bugs, noting where the stylets were inserted and the effort required to extract the mouthparts after the bug was disturbed. In addition to probing the stems and leaves of milkweeds, the overwintered adults were seen to feed on insect "carriage" (e.g. *Eleodes* beetles that had been struck by a car) and on the developing seeds of *Erodium cicutarium* (Geraniaceae). Caged adults were observed repeatedly to feed on carcasses of grasshoppers and of other milkweed bugs and to cannibalize freshly laid eggs. Twice I observed caged adults attacking and piercing conspecific adults that had been moving sluggishly. In another instance, a female, which had been brought in from the field the previous day, thrice pursued and attempted to pierce a teneral adult before she encountered and killed another adult that was lame.

The basal rosettes and crevices that provide shelter for the nymphs in spring also act to accumulate seeds and debris (including insect carcasses) that are blown or washed across patches of bare soil. In such situations, early instars often fed on the seeds of *Lepidium nitidum* (Cruciferae) and another, unidentified forb. Later instars also utilized the seeds of *Calandrinia ciliata* (Portulacaceae). Caged nymphs were seen to feed on dead grasshoppers and engage in various acts of cannibalism; first instar nymphs ate eggs and third instar nymphs impaled soft, freshly molted nymphs. In Napa County, California, K. Evans (personal communication) found nymphs feeding and developing on the seeds of a composite, probably *Achyrrachaena mollis*.

The *L. kalmii* population can certainly subsist and develop in spring and early summer without access to milkweeds. Two overwintered females, taken from the field on 23 April, were caged with mates and maintained on a diet of dead grasshoppers, seeds of *Calandrinia ciliata* and *Lepidium nitidum*, and water. One

of these females lived until 13 June and laid three clutches that each contained 12–34 viable eggs; the other lived until 8 July and laid four clutches that each contained 20–40 eggs. Three of these clutches were reared on the same diet given their parents; each of these produced several adults, which proved capable of mating and laying viable eggs without ever tasting a milkweed. The absence of milkweeds from the diet of a variable portion of the individuals in a population may help to account for the high variation in the cardenolide content of *L. kalmii* collected at different localities and seasons (Isman et al., 1977).

The adults of the spring generation fed voraciously after arriving in the milkweed stands. During June and July, they tended to concentrate on the inflorescences where they often probed flower buds and peduncles. When feeding on mature flowers, they tended to insert their mouthparts in the column (which covers the pollinia), rather than the hoods (which secrete nectar). Ants, *Crematogaster* sp., that were harvesting nectar sometimes displaced bugs from mature flowers by nipping at their beaks. Adult *L. kalmii* also fed from the major veins of leaves and on the tips of certain leaves where their repeated feeding (marked by wounds scabbed over by latex) caused yellowing.

During summer, adults frequently fed on insect tissues. The copious nectar produced by *A. eriocarpa* attracted abundant insects, many of which were trapped when their legs became jammed in the slits of pollinia and could not be withdrawn (Woodson, 1954, describes pollination in *Asclepias* spp.). Dead honeybees that had been ensnared in this manner were frequently scavenged by *L. kalmii*. On one occasion I observed adults feeding on honeybee carcasses lodged beneath a reduviid (*Apiomeris* sp.) that was ambushing pollinators at a milkweed inflorescence. Clusters of adults were also found feeding on dead ants, adult *L. kalmii*, and adults of the milkweed-feeding chrysomelid, *Chrysochus cobaltinus* LeConte. In light of the extensive literature on aposematism and the ecological chemistry of milkweed herbivores, it is interesting that *L. kalmii* is a predator on the immobile stages of other insects that feed on *Asclepias* spp. In the field, I observed five instances of adults feeding on the pupae of the monarch butterfly, *Danaus plexippus* Linnaeus, and one case in which two adults were feeding on a *D. plexippus* caterpillar (1 cm long) that was freshly killed. When leaves bearing clutches of *Chrysochus cobaltinus* eggs were introduced into a cage, an adult *L. kalmii* readily probed through the fecal case that was plastered over them and killed the eggs.

The pods of *A. eriocarpa* have thick, air-filled walls. As shown by Ralph (1976), such pods effectively protect the developing seeds from milkweed bugs. As a result, only a tiny portion of the milkweed seeds were available to *L. kalmii* until after mid-September. Prior to that time, the adults that fed on pods usually concentrated on the suture near the equator (see Ralph, 1976, for full description) and on small, aborted pods with walls damaged by chewing insects. Similarly, most of the nymphs that I found in August 1976 were associated with stems bearing pods in which the developing seeds had been partially exposed by gnawing insects. The exit holes left by pod-boring weevils, *Rhyssomatus* sp., frequently provide *L. kalmii* with access to developing seeds in Kansas, Minnesota, and New York (E. W. Evans and R. B. Root, unpublished observations). To simulate the damage observed at the Hastings Reservation, I clipped the tips off four scattered pods on 15 August 1976; when I returned on 17 August, each pod had

1–4 adults on it, and when I returned again on 19 August, each had 2–12 adults. Such heavy utilization of a resource made available by another herbivore illustrates the subtle interdependencies that can influence the structure of a plant-arthropod association.

An activity census that I made in a vigorous milkweed stand on the afternoon of 17 August 1976 gives an indication of how *L. kalmii* utilizes resources in summer. In this census, I walked across the stand and at every fifth stride, recorded the activity of every *L. kalmii* on the nearest milkweed stem and on the ground beneath it. Proceeding in this manner, I found 120 living adults (including 14 mating pairs), 8 dead adults, and no nymphs. Among the living, 66 were on milkweeds bearing pods, 40 were on milkweeds without pods, and 14 were on the ground or dried grasses. Of the 45 bugs that had their stylets inserted, 17 were feeding on pods, 15 on stems, 11 on leaves, 2 on dried flowers, 1 on a fallen dead leaf, and 1 on a *Danaus* pupa.

During the autumn, the bugs fed heavily on milkweed seeds, especially on those that had fallen to the ground. While some seeds were wafted far by the wind, most remained close to the parent plants. Often the down of individual seeds became matted together, producing wads of seeds that fell nearby. Even seeds with fluffy down that were shed individually usually travelled only a few meters.

DISPERSAL AND HOST LOCATION

Over most of the season adults flew infrequently and for distances of only a few meters. During late June and early July, however, when the adults of the spring generation entered the population, there was an obvious increase in flight activity. At this time hardened adults readily took flight when approached and teneral adults often basked, head upward, on the tips of tall grasses where they appeared to be readying themselves for launch. On two occasions I watched bugs flying along a relatively straight course, 2 to 4 m above the ground; in both cases the bugs covered at least 30 m before I lost sight of them. Some adults, however, can remain quite sedentary during this period. Thus, three adults, first marked on 13 June, were recaptured in almost the same location on 4 July; of course, these individuals could have undertaken a dispersal flight prior to their first capture.

Table 1. Conditions on days when dispersing *L. kalmii* adults were collected on the surface of a swimming pool. The weather instruments were placed 150 m from the pool; temperature was measured with a recording thermometer in an instrument shelter and sunshine was measured with a Campbell Stokes recorder.

Date	Total Catch of <i>L. kalmii</i>	Maximum Temperature (°C)	Duration of Sunshine (min)
14 June	15	30	700
15	17	24	706
18	1	20	672
19	1	17	262
20	31	24	712
21	28	26	708
3 July	2	20	670
6	12	29	668
7	12	29	668

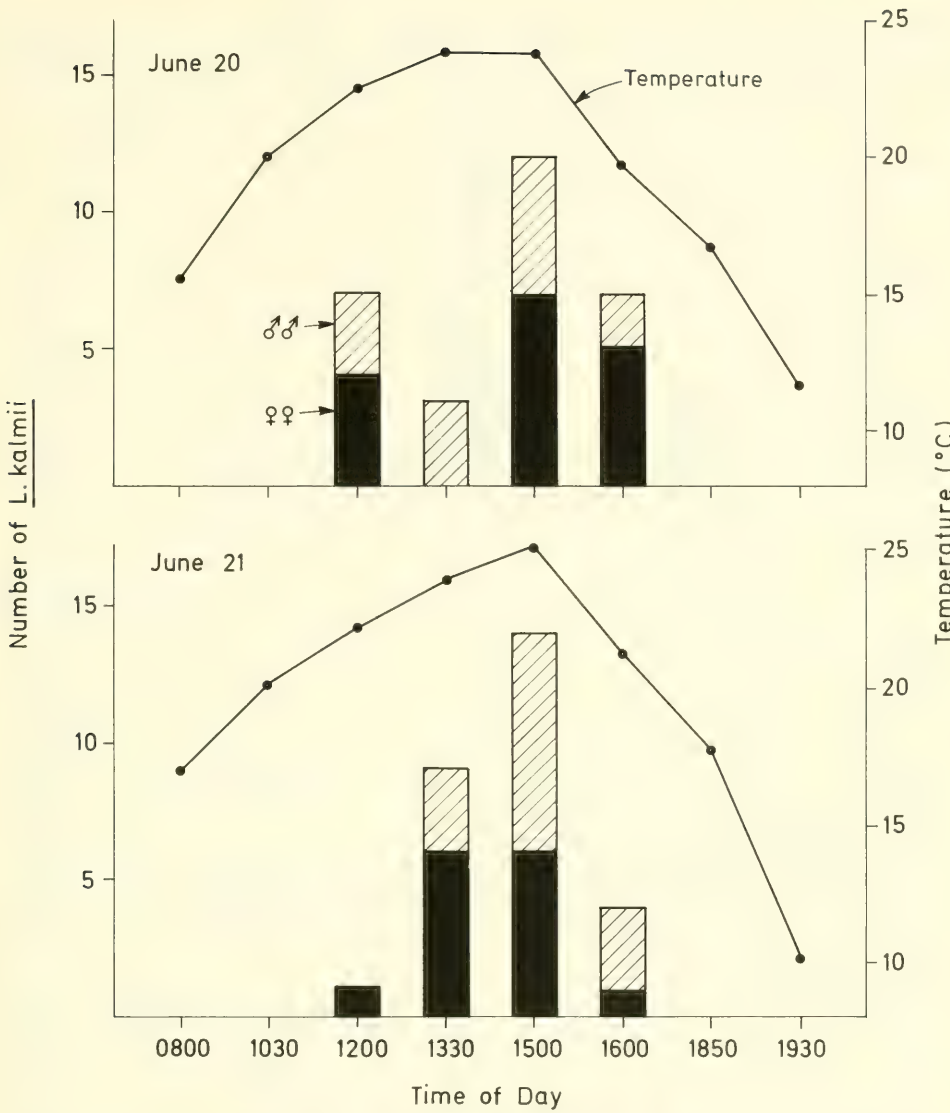


Fig. 3. Numbers of adult *L. kalmii* alighting in a swimming pool at different times of day. Temperatures were measured in an instrument screen. On both days, the sky was cloudless following the dissipation of morning fog prior to 0800.

Many of my observations on dispersal were made at a plastic swimming pool that was located 80 m from the nearest milkweed. I visited this pool, which had sides 125 cm high and a surface area of ca. 28 m², at intervals throughout the day and skimmed off all of the bugs that had dropped in since my previous visit. Bugs were first noticed in the pool on 13 June 1975. The largest collections were made on warm, sunny days (Table 1). Both sexes disperse and, judging from the alighting times, dispersal flights are undertaken chiefly during the late morning and afternoon (Fig. 3). No bugs were found in the pool on 13–21 July 1975, even though the weather was warm and clear during this period.

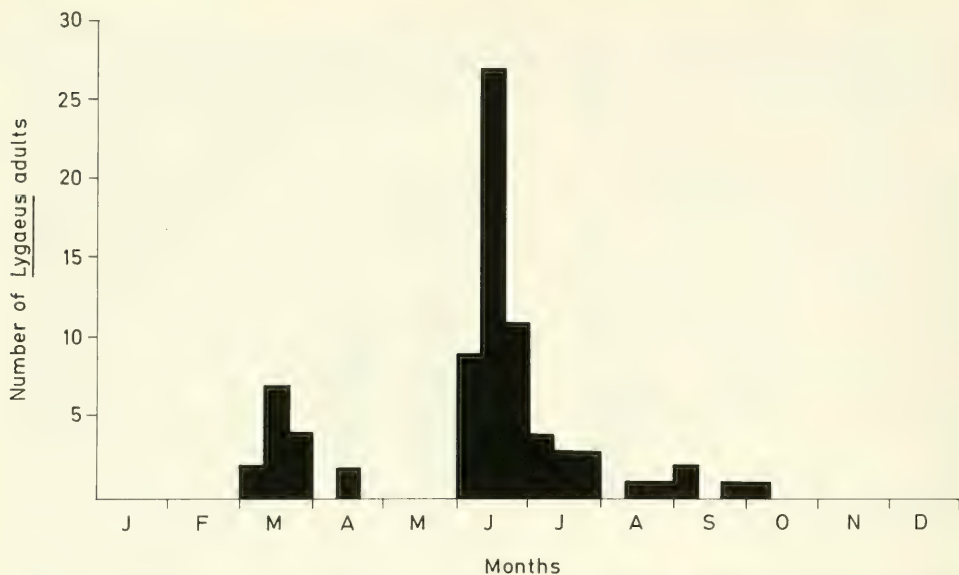


Fig. 4. Collections of adult *L. kalmii* alighting in nine elevated yellow-pan traps that were emptied weekly from January 1976 to December 1982. The bars denote the total numbers captured during the early, middle, and late portion of each month.

From 7 October 1975 through 10 August 1976, Walter Koenig collected the *L. kalmii* that alit in nine "yellow-pan" traps that were widely scattered in the grasslands at the Reservation. The pans, which were a "school-bus yellow" color and contained water and detergent (surface area = 864 cm²), were attached to posts so that the water level was at least 125 cm above the ground. These collections (Fig. 4) reveal that dispersal during 1976 occurred during the period when the teneral adults of the spring generation normally appear. Furthermore, these data suggest that there are flights in the very early spring, when the adults leave their winter quarters.

I carried out some simple experiments on host-finding behavior in 1975, during the period when the spring generation was dispersing. In each experiment, I stripped the leaves from a few milkweed plants and placed these, together with the chopped up stems, in small enamel trays. On sunny days, these trays were placed out in locations that were at least 100 m away from the nearest milkweed plant. Adults often located these trays within a few hours (Table 2). Since the chopped up plants bore little visual resemblance to a living milkweed, it seems likely that the bugs found the trays by using olfactory cues. On 6 July, I watched as late-arriving individuals approached a tray by flying in from a distance along a straight and level path. Since several bugs were already present at the tray, the possibility remains that such late arrivals were orienting to some cue given off by conspecifics.

ENEMIES

I saw only one case of predation in the field even though I observed many thousands of insects in the microhabitats utilized by *L. kalmii*. On 10 June 1975, I discovered an adult reduviid, *Rhynocoris ventralis* (Say) det. by J. L. Herring,

Table 2. Arrival of *L. kalmii* at trays containing freshly chopped up milkweed foliage and stems.

Date	Time Tray Set Out	Observations
21 June	1340	9 adults present at 1500
23 June	1300	2 adults present at 1345
6 July	1100	7 adults present at 1330, 5 more arrived the following hour
7 July		
Tray A	1200	No bugs present at either 1400 or 1515
Tray B	1200	4 ♀♀ collected at 1400, 4 new ♀♀ and 4 ♂♂ collected at 1515

feeding on a freshly dead, adult *L. kalmii*. On four occasions, I staged encounters in a cage during which *R. ventralis* adults easily killed vigorous, adult *L. kalmii*. Since two adult *R. ventralis* were maintained from 10 June–14 July on a diet of *L. kalmii*, it is clear that these predators can cope effectively with the cardenolides that the lygaeids contain at this season (Isman et al., 1977). Cannibalism, involving all life stages of *L. kalmii*, appears to be a relatively important cause of mortality (see Food Habits).

The aposematic traits observed in other milkweed bugs, e.g. *Oncopeltus* spp. (Root and Chaplin, 1976), are not so strongly expressed in *L. kalmii*. When suddenly approached or touched, *L. kalmii* adults often drop from vegetation and scurry under the litter or down rodent diggings. While the bugs are somewhat conspicuous when perched on milkweeds, individuals that are against a background of plant debris or broken soil can be easily overlooked.

I reared two parasitoids from ca. 125 field-collected adults and nymphs that were maintained in cages during the spring and early summer. A tachinid fly, *Hyalomya robusta* (Brooks) det. by C. Sabrosky, which had developed in an adult of unknown age, emerged on 26 June 1975. Another tachinid, *Leucostoma gravipes*

Table 3. Densities of major insects on *Asclepias eriocarpa* in Monterey County, California and on *Asclepias curassavica* near Cali, Colombia. All censuses are from samples of the terminal 30 cm from 50 stems. The study area in Colombia is described in Root and Chaplin (1976).

Locality:	California				Colombia				
	21 Jun 1975	6 Jul 1975	18 Aug 1976	4 Aug 1983	9 Feb 1971	19 Apr 1971	15 May 1971	12 Jul 1971	5 Aug 1971
Census Date:									
Dry weight of plants sampled (g):	498	516	692	ND	112	114	83	159	98
Numbers of:									
<i>Lygaeus kalmii</i>	105	117	37	49	0	0	0	0	0
<i>Lygaeus reclusius</i>	0	0	0	0	0	0	0	0	1
<i>Oncopeltus cingulifer</i> ¹	0	0	0	0	24	3	2	8	3
<i>O. unifasciatus</i> ¹	0	0	0	0	4	1	13	14	5
Undet. lygaeid nymphs	0	0	2	0	201	1	3	69	0
<i>Aphis nerii</i>	0	0	0	0	405	344	640	1544	1402
<i>Tetraopes basalis</i> ²	7	4	0	2	0	0	0	0	0
<i>Chrysochus cobaltinus</i> ³	1	2	1	6	0	0	0	0	0
<i>Danaus</i> spp. larvae	0	0	1	1	24	9	5	10	1

¹ Lygaeidae, ² Cerambycidae, ³ Chrysomelidae.

(Wulp.) det. by C. Sabrosky, which developed in an overwintered adult *L. kalmii*, emerged on 3 July 1975. The rate of parasitism I observed was much less than has been reported in midwestern populations (Simanton and Andre, 1936; Dingle, personal communication).

RELATIONSHIP TO MILKWEEDS AND THEIR FAUNA

Even though *L. kalmii* is polyphagous in the usual sense of the word, it has a special connection with milkweeds. This is reflected in the apparent ability of the adults to orient to milkweed odors, the concentration of adults in milkweed stands during June and July, and the prolonged reproductive diapause during June when milkweed pods are unavailable. The host relationships are thus broadly similar to those of *Lygaeus equestris* in Sweden (Solbreck and Kugelberg, 1972; Kugelberg, 1973, 1974); both species can survive and reproduce while feeding on a wide variety of seeds, but they are strongly associated with an asclepiadaceous host during those seasons when the plants are maturing pods and shedding seeds. They differ in that the Swedish bugs, which experience a relatively contracted and cool growing season, normally exploit a seasonal succession of hosts in completing only a single annual generation. In California, the extended season, coupled with the facultative host requirements of *L. kalmii*, results in at least two generations being produced each year which exploit milkweeds during different stages in their development.

During 1975 and 1976, *L. kalmii* was the most abundant insect on milkweeds in the Coast Range (Table 3, and other observations). The densities of *Lygaeus* spp. measured in Colombia (Table 3) and Illinois (Price and Willson, 1979) are much lower. The match between *L. kalmii* and conditions in the Coast Range tends to foster a heavy impact on milkweeds. As a consequence of its having a facultative diet, the number of adult *L. kalmii* produced by the spring generation depends, to a large extent, on factors that are unrelated to the status of the "preferred" milkweed host. The environment at the Hastings Reservation usually provides an abundance of requisites for this generation; extensive rodent diggings create disturbances where weed seeds abound in close proximity to bare areas used for basking and the normally sunny weather of spring promotes early and rapid development. The adults of this generation emerge when *A. eriocarpa* stands out as a succulent "oasis" in the drying grassland. Here it should be emphasized that *A. eriocarpa* is a long-persisting, summer perennial; thus it lacks the attributes of successional and "non-apparent" plants that have been used to interpret the ecology and evolution of milkweed insects in other regions (e.g. Caldwell, 1974; Price and Willson, 1979).

After the spring adults shift to *A. eriocarpa* in June, *L. kalmii* is capable of producing herbivore loads that are quite high as compared with the loads measured on milkweeds in other temperate zone localities (Table 4); the factors promoting the heavy loads observed in tropical Colombia are discussed in Root and Chaplin (1976). Throughout the early summer of 1975, the density of *L. kalmii* at the Hastings Reservation consistently exceeded two adults per stem and it was often much higher in the smaller milkweed stands (the data reported in Tables 3 and 4 are from the Arnold Field, the most extensive stand in the vicinity). The arrival of these adults in the milkweed stands several weeks before the seeds become available serves to further increase their impact. Their intense feeding on the

Table 4. Herbivore loads on milkweeds at several localities in North and South America. The loads are expressed as the mg (dry wt) of herbivores (excluding nectarvores) per 100 g (dry wt) of plant material. The data come from samples of the terminal 30 cm from 50 stems growing in large milkweed stands.

Locality	Host	Sample Date	Plant Phenology		Herbivore Load (mg/100 g)
			Flowers	Pods	
California	<i>A. eriocarpa</i>	21 June	+	○	277.5
		6 July	+	○	428.6
		18 Aug	+	+	38.4 ¹
Colorado	<i>A. speciosa</i>	8 Aug	+	+	110.7
		9 Aug	+	+	70.5
Missouri	<i>A. syriaca</i>	17 Aug	○	+	36.5
		18 Aug	○	+	50.3
New York	<i>A. syriaca</i>	26 July	+	+	4.3
		30 July	+	+	32.5
		7 Sept	○	+	42.4
Colombia	<i>A. curassavica</i>	9 Feb	+	+	559.3
		19 Apr	+	+	303.9
		15 May	+	+	312.3
		10 July	+	+	505.2
		5 Aug	+	+	292.5

¹ Samples taken on a day of unseasonable rain and cold.

All other samples in the table were taken on clear, warm days during the late morning.

plants' reproductive tissues causes many flowers to wither prematurely and probably accounts for the complete failure of the pod crop in several small stands during 1975 and 1976. Furthermore, these voracious adults feed heavily on the inactive and sluggish stages of other insects. Since *L. kalmii* can utilize milkweeds containing cardenolides that are toxic to many other animals, it is not surprising that the adults readily attack other milkweed herbivores that sequester these compounds (see list in Rothschild, 1973), such as *Danaus plexippus* at the Reservation and *Oncopeltus fasciatus* in the eastern United States (Ralph, 1977). This combination of great abundance, omnivorous habit, and indifference to cardenolides makes *L. kalmii* a potentially serious threat to any milkweed insect that must pass through vulnerable life stages during July and August. In this regard, it is interesting that *D. plexippus* was relatively rare at the Hastings Reservation during my investigation (Table 3 and other observations) even though its famous overwintering sites at Pacific Grove, California, are nearby and that *O. fasciatus* has never been observed at the Reservation even though abundant populations occur elsewhere in California (K. Evans, personal communication). The possibility that *L. kalmii* can limit the populations of milkweed specialists has several interesting implications that warrant further investigation.

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RECOGNITION OF TWO SPECIES IN THE PINE FEEDING
"NEODIPRION FULVICEPS COMPLEX" (HYMENOPTERA:
DIPRIONIDAE) OF WESTERN UNITED STATES

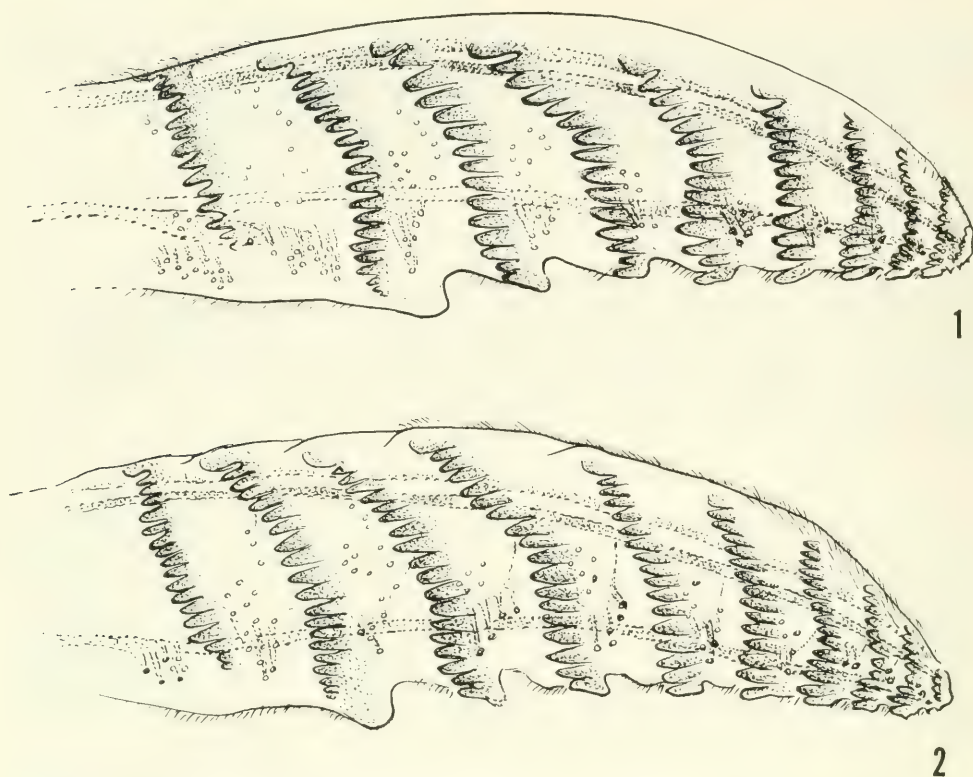
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Abstract.—Two species are recognized in the *Neodiprion fulviceps* complex as previously defined. Biological differences in Arizona populations on *Pinus ponderosa* and subsequent discovery of consistent differences in the morphology of the female lancet and coloration of the females and larvae support this separation. *Neodiprion fulviceps* (Cresson) is restricted to those populations that emerge as adults in the spring and overwinter as prepupae in a cocoon. *Neodiprion autumnalis*, n. sp., is described for those populations that emerge as adults in the fall and overwinter as eggs in the needles.

Most western populations of *Neodiprion* associated with *Pinus ponderosa* Dougl. ex Laws., as well as *Pinus jeffreyi* Grev. & Balf. and some other pines, have been referred to the "*Neodiprion fulviceps* complex" based on Ross's (1955) definition. This complex has been very confusing due to apparent biological differences between different populations and the lack of consistent morphological features for adults or larvae upon which to segregate species. Regarding this, Ross (1955) stated "Large numbers of collections from *Pinus ponderosa* provide the most puzzling questions in this genus. It is possible that all these are in a single species, perhaps represented by a number of fairly well-marked geographic races. If so the name *fulviceps* (Cresson) described from Nevada, might apply."

Biological data and comparisons of adults and larvae are necessary to help unravel some of the problems. A study in Arizona by the junior author revealed distinct differences in the biology of two populations (Wagner et al., 1986). Further studies revealed color and structural characters in the female and coloration of the larvae that could also be used to separate individuals of the populations. These differences were consistent within the different populations studied by the junior author and warrant recognition of two distinct species. Adults of both are referred to the *N. fulviceps* complex of Ross. Study of the type of *L. fulviceps* Cresson, the lancet of which had never been removed and examined, revealed that the name *fulviceps* applies to the species which overwinters in a cocoon and emerges in the spring. The other populations, those in which adults emerge in the fall and overwinter in the egg stage, are here regarded as a new species. These two species are



Figs. 1, 2. Female lancets. 1, *Neodiprion autumnalis*. 2, *N. fulviceps*.

separated and described and *N. fulviceps* is defined and restricted to a smaller group of *Neodiprion* than that which Ross (1955) defined. The present work does not solve all the problems in the complex, but does verify the existence of more than one species and solves the immediate problem of the Arizona populations. It should be emphasized that taxonomic work on and the identification of the western *Neodiprion* populations cannot always be based on morphology alone; associated biological data are of utmost importance.

THE "*NEODIPRION FULVICEPS* COMPLEX"

Ross (1955) defined the *fulviceps* complex in his key, essentially by the following characters: mesoscutellum nearly impunctate (as all species of the *sertifer* group); occurring west of the 100th meridian; annuli 3 and 4 of female lancet end above rod (not below rod as in *N. demoides* Ross); dorsum light, red or red yellow (dorsum black or mostly black, head black or with black stripe between eyes in *N. gillettei* (Rohwer), *N. mundus* Rohwer, and *N. ventralis* Ross); scopa long (not short as in *N. edulicola* Ross); and larger species, 10–11 mm long that feeds on *Pinus ponderosa*. Though coloration is commonly variable in sawflies, and size and host are not always characteristic, comparison of the specimens of the Arizona populations with those species in couplets 28–33 of Ross' key excluded them from other species and placed them within his definition of *N. fulviceps*. There being only one name available in the *fulviceps* complex, the type of *fulviceps* was bor-

rowed and the female lancet was pulled out and examined to determine which, if either, of the Arizona populations the name *N. fulviceps* might apply. It was discovered that *N. fulviceps* was identical to the populations that overwinter as cocoons and that emerge as adults in the spring of the following year; it is a generally dark species and is apparently a species that is not as common in the West as the other population described below as *N. autumnalis*.

Reared material of the *fulviceps* complex in the National Museum of Natural History was studied, and most all must be referred to *N. autumnalis* based on characters of the female lancet as well as emergence dates of the adults. This includes specimens from Willits, California, for which Dahlsten (1961) reported biological data. Using *N. fulviceps* in the restricted sense as here defined, *N. autumnalis* replaces *N. fulviceps* as the more common complex in the West, a complex that may eventually be broken down further as more information becomes available. Dahlsten's (1966) study of "*fulviceps*" in several study areas in California on *Pinus jeffreyi*, *P. ponderosa*, and *P. radiata* have a life cycle similar to *N. autumnalis* and examination of some of the specimens on which Dahlsten's study is based showed that they belong to this complex. However, Dahlsten found differences in the populations studied including number of eggs per female, number of needles in each fascicle used for oviposition, number of eggs inserted in each needle, spacing of egg pockets, egg color, number of feeding instars, dates of larval eclosion, larval size, and larval feeding capacity. Because Dahlsten found no morphological characters coinciding with these differences, it is difficult to assess their importance. At present, the name *autumnalis* may be applied to individuals of the populations studied by Dahlsten.

Neodiprion fulviceps (Cresson)

Lophyrus fulviceps Cresson, 1880: 25.

Type female.—Length, 9.0 mm. Head dark orange with narrow black stripe between ocelli, darker orange than pale areas of thorax and legs; antenna black, scape slightly paler. Thorax with pronotum and mesepisternum whitish, mesonotum mostly black with sutures and scutellum lighter black to gray; metanotum black; remaining parts dull orange. Abdomen black above, with whitish lateral longitudinal stripes; venter pale orange. Legs light orange with bases of tibiae and coxae more whitish. Wings hyaline; veins brownish to black, costa and stigma paler, more orange. Antenna 18-segmented. Lancet as in Fig. 2 (drawing from Arizona populations and compared with type of *fulviceps*); characterized by features given in Table 1.

Arizona populations.—Agreeing with type in structure and most color characters. Color somewhat variable, especially amount of black on mesonotum which at one extreme may be restricted to black marks on the lateral lobes and prescutum; darkest extreme is that of the type specimen. Abdomen usually black dorsally and venter sometimes suffused with black. Typical specimens examined from Arizona slightly paler than type.

Male.—Similar to *N. autumnalis*.

Larva.—Late instar length, 17–22 mm. Head orange with eyespot black, sometimes with blackish mark on frons; thoracic legs mostly black (femora, tibiae, and tarsi may be whitish to orange, but not as dark orange as head). Body with 2

Table 1. Comparison of characters separating *Neodiprion autumnalis* and *N. fulviceps*.

	<i>N. autumnalis</i> , n. sp.	<i>N. fulviceps</i> (Cresson)
Lancet:	Fig. 1. 1st and 2nd annuli farther apart; 1st annulus shorter, usually with 10–11 teeth. Annuli 3–5 end near top of rod. Teeth of 3rd annulus about same size. Serrulae 1 and 2 straighter. 1st serrula longer than its depth.	Fig. 2. 1st and 2nd annuli closer together; 1st annulus longer, usually with 15–16 teeth. Annuli 3–5 overlap rod and end near dorsal edge of lancet. Ventral teeth of 3rd annulus usually larger than dorsal teeth. Serrulae 1 and 2 more directed ventrally. 1st serrula as long as or shorter than its depth.
Color:	Head and pale markings of thorax and legs more uniform. Mesonotum usually pale orange with black streaks on lateral lobes. Abdomen mostly orange with whitish lateral longitudinal stripes, sometimes blackish dorsally.	Head usually much darker orange than pale orange to whitish markings of thorax and legs. Mesonotum mostly black, prescutum sometimes paler and scutellum and sutures white to orange. Abdomen commonly black or mostly black dorsally with more contrasting lateral longitudinal stripes.
Larva:	Fig. 3. Head orange, usually median black streak on dorsum. Body without black below spiracles.	Fig. 4. Head orange, sometimes blackish on frons. Body usually with two black stripes, sometimes broken into spots, below spiracles.
Biology:	Overwinters as egg; adults emerge in fall of same year.	Overwinters as prepupa in cocoon; adults emerge in spring of following year.

subdorsal longitudinal black stripes and usually with 2 subspiracular black stripes, though one just below spiracles may be light or broken (Fig. 4).

Biological data.—On *Pinus ponderosa*. Larvae feed in spring and early summer, overwinter in cocoons in the soil, and adults emerge early the following spring (Wagner et al., 1986).

Type.—Female, at The Academy of Natural Sciences of Philadelphia, Pennsylvania, labeled “Nev.,” “Type No. 292.1.”

Specimens examined.—Arizona, nr. I-40, Flagstaff, Coconino Co., VII-21-1982, pupated by VII-29-1982, emerged by V-16-1983 to V-20-1983. About 60 specimens examined.

Notes.—See Table 1 for differentiating features of the female lancet. This in conjunction with Fig. 2 should characterize *N. fulviceps*. The Arizona specimens are the only ones I have seen that I can associate with this species.

Neodiprion autumnalis Smith, NEW SPECIES

Female.—Length, 8.5–10.0 mm. Head orange, similar to orange markings of thorax and legs; narrow black mark between ocelli and narrow black streak in each lateral suture of postocellar area; antenna black with scape, pedicel, and all or most of 1st flagellar segment reddish brown. Thorax pale orange with black



Figs. 3, 4. Larvae. 3, *Neodiprion autumnalis*. 4, *N. fulviceps*. (Photographs by M. R. Wagner.)

stripes on each mesonotal lateral lobe; posttergite and metanotum black; sometimes blackish or infuscated area on mesoprescutum. Abdomen pale orange with whitish lateral longitudinal stripes, sometimes blackish marks at center of terga. Legs pale orange with basal $\frac{1}{4}$ of tibiae and coxae more whitish. Wings hyaline; veins brownish, stigma paler to orange. Antenna 16–19 segmented. Lancet as in Fig. 1, characterized by features given in Table 1. Scopa of sheath as in Fig. 25 of Ross (1955).

Male.—Length, 7.5–8.5 mm. Black; labrum and legs beyond coxae yellow orange.

Larva.—Late instar length 17–22 mm. Head orange with eyespot black, usually with black medial stripe on dorsum. Thoracic legs orange, black only lining edges of sclerites; black ventral stripe usually present between thoracic legs to abdomen. Body with subdorsal black longitudinal stripes; no black below spiracles (Fig. 3).

Biological data.—On *Pinus ponderosa*. Adults emerge in the fall and oviposit; eggs overwinter in the needles, and larvae hatch and feed in the spring (Wagner et al., 1986).

Holotype.—Female, labeled “Springerville, Apache Co., AZ, VIII-13-1981, coll.

as pupa in soil, on *Pinus ponderosa*, coll. by M. R. Wagner." In the National Museum of Natural History, Washington, D.C.

Paratypes.—Springerville, Arizona, collected as larvae VII-8-1982, pupated by VII-21-1982, emerged XI-1982 (27 ♀, 32 ♂); Springerville, Arizona, collected as larvae VII-14-1980, emerged Nov. 1980 (12 ♀, 3 ♂); Camp Verde, Yavapai Co., Arizona, collected as larvae V-18-1981, pupated VI-1981, emerged XI-XII-1981, on *Pinus ponderosa* (5 ♀, 2 ♂); 5.0 mi S Flagstaff, Coconino Co., Arizona, collected as larvae V-26-1981, pupated VI-1981, emerged XI-XII-1981 (3 ♀, 1 ♂). In the National Museum of Natural History, Northern Arizona University, and the Canadian National Collection, Ottawa.

Notes.—Comparison of characters in Table 1 and Fig. 1 will differentiate this species from other species of *Neodiprion*. The lancet is similar to that of *N. ventralis* Ross in that the first serrula is rather long. However the first serrula of *N. ventralis* is much larger, nearly twice as long as its depth, whereas the first serrula of *N. autumnalis* is only slightly longer than its depth. I have not found characters in males to separate them from males of other species.

I have seen specimens from California, Oregon, and Montana that may be referred to this species.

ACKNOWLEDGMENTS

With thanks to Donald Azuma, The Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, for allowing study of the type of *fulviceps* and to D. L. Dahlsten, University of California, Berkeley for loaning some *Neodiprion* specimens. My wife, J. L. Smith, prepared illustrations 1 and 2. I appreciate the help of the following reviewers: R. E. White and E. E. Grissell, Systematic Entomology Laboratory, Agricultural Research Service, Washington, D.C.; G. Gibson, Biosystematics Research Institute, Agriculture Canada, Ottawa; and D. G. McCullough, School of Forestry, Northern Arizona University, Flagstaff.

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**LIFE HISTORY OF *NEODIPRION FULVICEPS* (CRESSON),
A PONDEROSA PINE FEEDING SAWFLY
(HYMENOPTERA: DIPRIONIDAE)**

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Abstract. — The life history of *Neodiprion fulviceps* Cresson, as a distinct species in the *Neodiprion fulviceps* complex, is described. The larvae feed on the foliage of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws. Overwintering occurs as cocoons in the soil. There are four male and five female feeding larval instars. Development from egg hatch to adult emergence requires 47 days for males and 54 days for females. Behavioral characteristics of adults and larvae are described.

Conifer-feeding sawflies in the family Diprionidae are major economic pests of natural and plantation forests. Life histories for diprionid sawflies in eastern United States are well known (Wilson, 1977). However, pine feeding Diprionidae in western United States are not well understood. For example, of the five species of sawflies that feed on ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., in Arizona, detailed life history information is available for only one species.

In addition to the paucity of basic biological information, the taxonomy of this group is confused. Ross (1955) groups several variable populations of sawflies feeding on pines into the *Neodiprion fulviceps* complex. Smith (see preceding paper in this journal) separates at least two species from the *N. fulviceps* complex: *N. fulviceps* and *N. autumnalis* Smith. Biological data on the *N. fulviceps* complex presented by Dahlsten (1961, 1966, 1967) is similar to our biological observations on *N. autumnalis*. It is likely that the *N. fulviceps* complex studied by Dahlsten (1961, 1966, 1967) is more closely related to *N. autumnalis* than *N. fulviceps*.

This paper reports preliminary biological information on *Neodiprion fulviceps* as a distinct species within the *N. fulviceps* complex.

MATERIALS AND METHODS

Data were collected from and biological observations made on a single outbreak population of *N. fulviceps* located on the median strip of Interstate 40, south of Flagstaff, Arizona. The population was discovered in July 1982. The area was a typical ponderosa pine transition zone with pole-sized open grown trees.

Life history, adult and larval behavior. — Observations on the development stage of the insect and behavior were made on weekly visits to the infested area from July 1982 through July 1985. The earliest and latest observation of a particular life stage in the field, taken over the four year study period, were used to determine the life history.

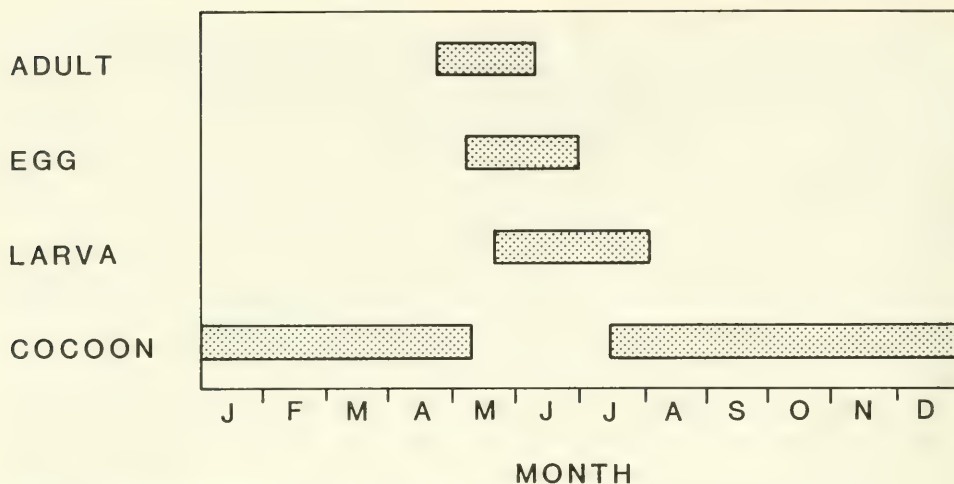


Fig. 1. Seasonal periods for *Neodiprion fulviceps* life stages in the field from 1982-1985.

Oviposition.—A sample of 50 needle clusters from 11 trees were collected and examined in June 1983. The following was noted for each egg cluster: needle length, number of eggs, presence or absence of a test slit and the number of needles in a fascicle that held eggs.

Larval instars and development.—Visits were made to the study area in May and June 1984 to determine the number of larval instars, average head capsule width for each instar and development time. At each visit, eggs were located and observed until hatching occurred. Newly hatched sawflies were carefully collected and placed in plastic rearing boxes for transport to the laboratory where the head capsule widths were measured with a microscope micrometer. Individual sawfly larvae were then placed in numbered petri dishes with fresh ponderosa pine foliage. Fresh foliage was supplied every other day. Petri dishes were kept in a Percival® temperature chamber at 25–27°C and photoperiod of 16 h light-8 h dark. Each sawfly was checked daily until it spun a cocoon. The date and the width of the head capsule were recorded following each molt. Numbered cocoons were transferred to a desiccation jar containing a small amount of water. As the adult sawflies emerged, they were sexed and transferred to a freezer for storage.

RESULTS AND DISCUSSION

Life history.—Fig. 1 illustrates the periods during which various life stages of *N. fulviceps* have been observed in the field. These observations contrasted sharply with Dahlsten's (1961) description of the life history of the *N. fulviceps* complex where he reported that the adults emerge in the fall and the eggs overwinter. The life cycle differences between these species and the resulting reproductive isolation were the basis for initially questioning the species identification of this sawfly population. Subsequent taxonomic evaluation (see preceding paper) yielded sufficient morphological variation to allow separation of *Neodiprion fulviceps* as a distinct species within the *N. fulviceps* complex.

Adult behavior and oviposition.—Adult emergence began in late April and continued through the end of May. Males were active flyers and able to maintain

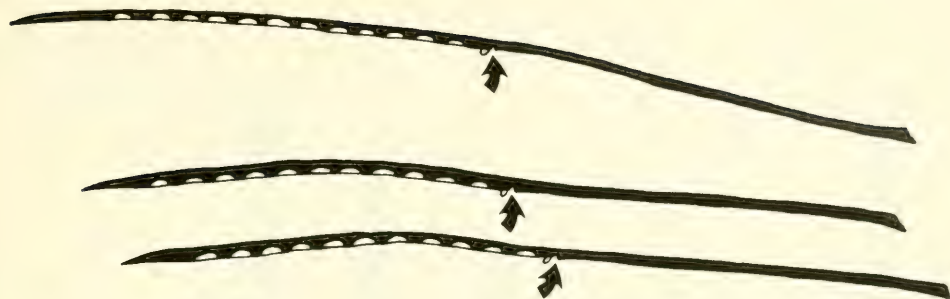


Fig. 2. Ponderosa pine needles with *Neodiprion fulviceps* eggs. Arrows indicate test slits cut by females.

flight in strong wind. The males were usually seen swarming around the outer crown of the tree. Females were rarely observed in flight; they were generally found either stationary or walking up and down needles on exposed twigs.

Very little courtship behavior was observed. A male that landed near a female immediately attempted to copulate. Males also attempted to mate with ovipositing females. In the laboratory, mating and oviposition occurred in as little as one hour after emergence of the female. Adults usually lived two to three days in the laboratory.

The adult female began oviposition by cutting a small slit near the base of the needle. Similar oviposition behavior has been described by Dahlsten (1961) for the *N. fulviceps* complex, and by Benjamin (1955) for *N. lecontei* Fitch. This small cut is referred to as a test slit (Fig. 2). The function of the test slit is unknown but it may be cut by the female to sever the resin duct or determine suitability of the needle for oviposition. The test slit was always made proximal to the part of the needle in which oviposition occurs. Of 68 individual needles containing eggs, 67 included test slits. The one needle that did not have a test slit was next to a needle that did have a test slit. Some needles were found with test slits and no eggs. Apparently, the female rejected some needles after sawing into them. Frequently, a drop of resin was observed where the test slit was cut into the needle.

Females laid an average of 10.81 eggs per needle ($SE \pm 3.99$, range 1–18, $n = 68$). An average of one egg was laid for each 1.12 cm of needle length. Typically, eggs were oviposited only into the distal one half of each needle. Ponderosa pine usually has three needles per fascicle. Of the three-needle fascicles we evaluated, 86% had only one needle in the group with eggs and 14% had two needles in the group with eggs. Eggs were never found in all three needles of a fascicle.

Larval behavior.—The eggs split open and the larvae emerged from the eggs head first, usually facing the tip of the needle. This behavior was almost identical to that described by Ghent (1960) for *Neodiprion pratti banksianae* Rohwer. The whitish-yellow head capsule quickly darkens to a smokey grey color.

Early instar larvae fed as a group around individual needles facing the needle tip. As many as eight larvae were observed feeding at a single point on a needle. Only previous years' foliage was available to early instar larvae on the tree. During later instars, the current year's foliage was available but larvae rarely fed on it.

The initial outbreak of *N. fulviceps* occurred on what would be classified as

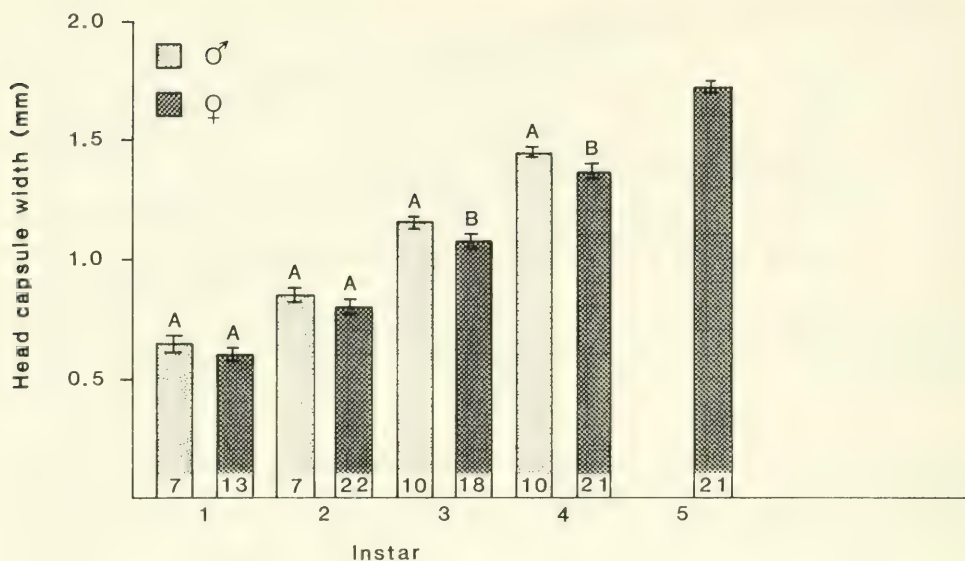


Fig. 3. Head capsule widths by instar for male and female *Neodiprion fulviceps* larvae. Bars indicate $\pm$ standard error of the mean. Different letters above the bars indicate significant differences between sex within an instar (ANOVA, $\alpha = 0.05$). Values at the base of bars indicate sample size.

typical sawfly susceptible trees, i.e. open grown pole-sized trees (dbh $\bar{x}$ = 9.1 inches, SE = 3.71, range 5.5–16.6). In 1985, however, the infestation had expanded to include trees of a substantially larger size class (dbh = 26.6, SE = 3.78, range = 19.2–31.6). The expanded infestation occurred primarily on open grown trees as well. The ability of *N. fulviceps* to colonize large (older) trees may be unique among pine-feeding Diprionidae in the Southwest.

Pine-feeding Diprionidae are well known for their larval defensive behavior. Typically larvae rear their heads, often in unison, and emit a droplet of resin on a predator or parasite. This defensive behavior was observed for *N. fulviceps* in the early instars. In later instars, however, the typical defensive strategy was almost completely replaced by a quite strange behavior. When late instar larvae were disturbed they completely released their hold on feeding sites and dropped from the trees. We were able to collect larvae very easily by holding a container beneath a feeding branch and simply tapping the branch. This behavior was observed in the penultimate instar (last feeding instar) and the ultimate instar, but it was not determined if larvae that dropped from trees in this manner returned to the tree, ceased feeding and spun cocoons, or died.

Larval instars and development.—Rearing individual larvae from eclosion to adults indicated there are four feeding instars for the male and five feeding instars for the female (Fig. 3). The ultimate non-feeding instar, common in many sawfly species, also occurs in *N. fulviceps*. Because of the short duration of this nonfeeding instar, we did not measure the head capsule width. The third and fourth instar males were statistically larger than females.

The cumulative time in each of the main development stages was determined (Fig. 4). Males and females spent statistically equal amounts of time in the first

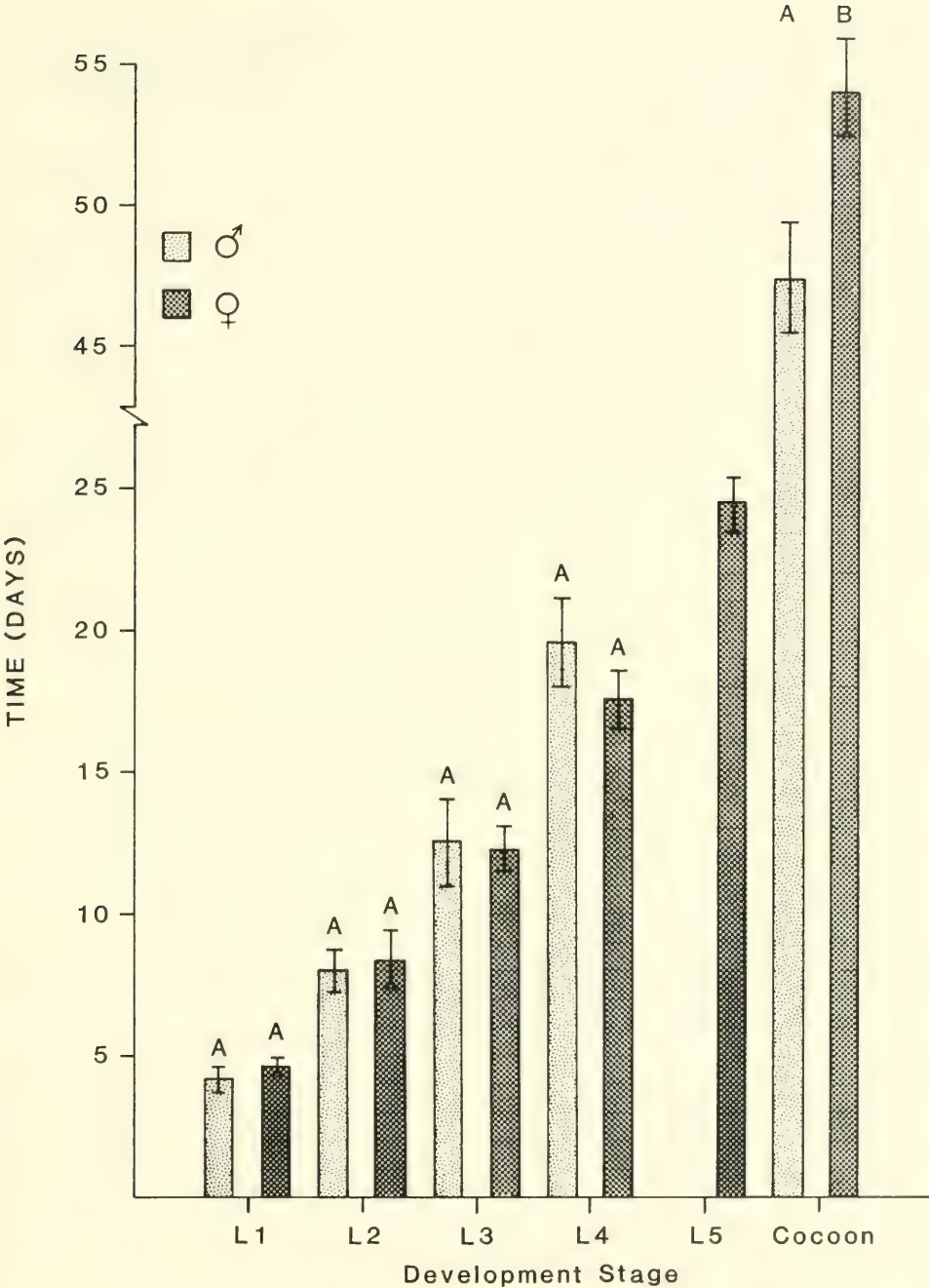


Fig. 4. Cumulative time from egg hatch to the end of selected development stages of *Neodiprion fulviceps* reared at 25–27°C. Bars indicate $\pm$ standard error of the mean. Letters above the bars indicate a significant difference between sexes within a development stage (ANOVA, $\alpha = 0.05$). Sample size: L 1–5, 6 males-11 females; cocoon, 3 males-6 females.

four instars. The adult females require 54.0 ± 1.63 days to complete development compared to 47.3 ± 1.67 days for males (based on smaller sample, $n = 6,3$ respectively). This explained the commonly observed early emergence of males. Males were in the cocoon stage approximately 27 days and females approximately 29 days.

The development periods reported in Fig. 4 are from 17 individuals (six males, 11 females) that were reared from first instar larvae to cocoon. The initial sample size was 60 larvae. Of the 60 larvae, 29 successfully spun cocoons (only 17 were used in the development study because the molting date was missed for some individuals). Of the 29 cocoons only nine emerged as adults during the study. The poor survival of individual larvae was probably due to the inability of individual larvae to initiate feeding sites on the ponderosa pine foliage. Colonial feeding by sawfly larvae is thought to be a mechanism of dealing with the tough needles; the first larva that successfully chews into the needle is typically joined by several others (Ghent, 1960). Thus, rearing larvae in isolation may contribute to low survival rates. The poor adult emergence was possibly due to low relative humidity in the rearing containers, or improper temperature or photoperiod during the larval period.

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NEW AND LITTLE KNOWN APHIDS FROM MEXICO.
8TH NOTE*: A NEW *CINARA* (HOMOPTERA: APHIDIDAE)
LIVING ON *PINUS* WITH A REDESCRIPTION OF
CINARA LOUISIANENSIS BOUDREAUX

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Abstract. — Two of the many species of *Cinara* collected in Mexico are discussed and illustrated. *C. louisianensis* Boudreaux is redescribed with comments on its status relative to *C. idahoensis* Knowlton and compared with *C. tujafilina* with which it shares the rare character of pale femorotibial joints. *C. brevopilosa* n. sp. is described and distinguished from the morphologically similar *C. glabra* Gillette and Palmer.

Aphids in the genus *Cinara* feed strictly on conifers in Pinaceae and Cupresaceae. They have been found throughout the world where conifers are native (generally the northern hemisphere) and more recently in the southern hemisphere where extensive plantations of conifers have been established for the forest industry. These aphids are relatively large, often with long mouthparts, and feed on twigs, cones, trunks and roots of their hosts. About 175 species are known to occur in North America north of Mexico and, since Mexico not only shares common coniferous species with the United States as well as having its own distinct set of conifers, it would be expected that many species known in the United States might be found there as well as new species. Over the past few years the authors have made many collections of *Cinara* in Mexico. Unfortunately not all could be determined to species primarily because of limited information on the variability within named species. The two species treated in this paper are distinct enough to warrant discussion. One is a new record for Mexico and matches a poorly known aphid previously found only in southeastern United States, the other is a new species.

***Cinara louisianensis* Boudreaux 1948**

Figs. 1A–B, 2

Eastop and Hille Ris Lambers (1976) relegated this species without comment to a new, junior synonym of *C. idahoensis* Knowlton (1935) (see discussion). With

* Remaudière, G. and F. W. Quednau 1985. Pucerons nouveaux et peu connus du Mexique. 7^e note: Deux nouvelles espèces des genres *Myzocallis* et *Stegophylla* (Homoptera: Aphididae). Rev. Fr. Entomol. (N.S.) 7: 118–124.

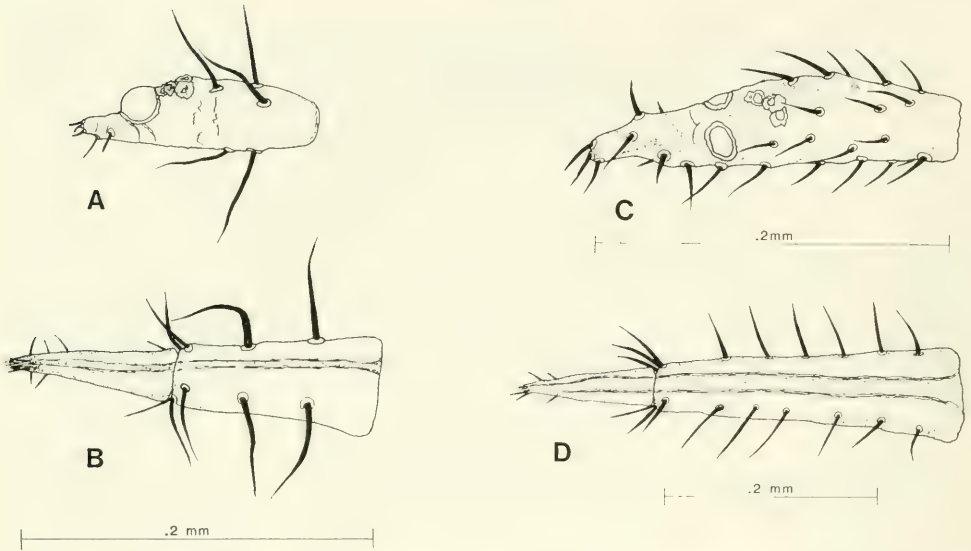


Fig. 1. *Cinara lousianensis*. A, Antennal segment VI. B, Ultimate rostral segment. *Cinara brevopilosa*. C, Antennal segment VI (note separation of satellite and primary sensoria). D, Ultimate rostral segment. Drawn by D. Voegtlin.

additional characters now used to discriminate among species of *Cinara*, a modern description of *C. lousianensis* is provided based on some paratypes and the specimens from Mexico.

Apterous viviparous females (described from 14 specimens). — *Color in life*: No information on the specimens from Mexico was recorded, but Boudreaux (1948) gives the following: "Apterous viviparae similar to alatae except that the first three antennal segments are lighter, the white powdery areas are scattered more widely over the abdomen and the thorax is green."

Color of mounted specimens: Entire body with little discernible sclerotization (Fig. 2A). Tip of antennal (IV), V, distal $\frac{1}{2}$ of VI, rostral segments III–V, tip of tibiae, tarsi (Fig. 2D) and dorsal body setae darker than body; head, legs, siphunculi, cauda, anal, subgenital and spiracular plates, and intersegmental sclerites slightly darker than body. Joint of femora and tibiae pale.

Morphology: Antennae about $\frac{1}{3}$ length of body with 0–1 secondary sensoria on V, 0 on III and IV; rostrum about $\frac{2}{5}$ of the body, ultimate rostral segment a little shorter (0.85–0.99) than the 2nd metatarsus. Mesosternum without tubercle. Cauda broadly triangular (Fig. 2H).

Chaetotaxy: Antennal setae stout, 5–6 on II, 11–16 on III (longest 51–86 μm), 6 on base of VI, 2 preapical setae on process terminalis (Fig. 1A); rostral IV with 4 accessory setae (Fig. 1B). Tibiae with dorsal setae much stouter and longer (83–150 μm on metatibia) than those on other sides (Fig. 2G). Dorsal setae on each abdominal segment more or less distributed in two irregular lines, varied in size and shape, from short and fine to long, stout spine-like, the longest often on pale sclerites approximately $5 \times$ diameter of base of seta; tergite V with 24–36 setae (the longest 61–102 μm), VIII with 8–13 (length 120–140 μm); siphuncular setae

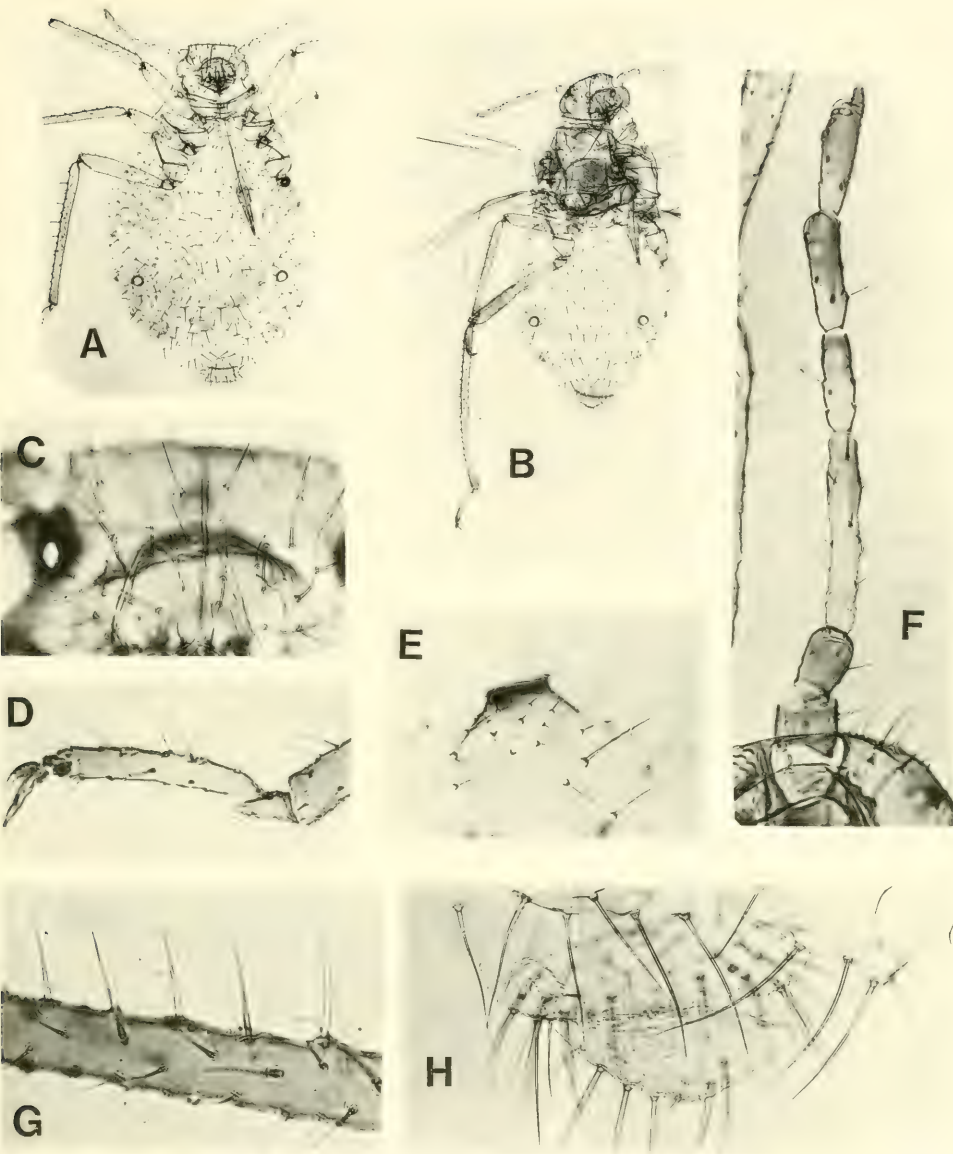


Fig. 2. *Cinara louisianensis*. A, Apterous viviparous female. B, Alate viviparous female. C, Vertex and front of head of aptera. D, First and second segments of metatarsus of aptera. E, Siphuncular cone of aptera. F, Antenna of alate. G, Section of metatibia of aptera. H, Tergite eight and cauda of aptera. Photography by G. Remaudière.

distributed evenly over cone, of uniform shape, but increasing in length near base (Fig. 2E); cauda with 5–6 stout setae plus 4–6 much smaller and finer ones; subgenital plate with about 20 setae. Ventral abdominal setae fine, of near uniform size and shape throughout.

Measurements: Table 1.

Alate viviparous female (described from 34 specimens).

Color in life: No notes made from Mexican material. Boudreaux (1948) gives

Table 1. Morphometric data on *Cinara louisianensis* and *C. brevipilosa*. All measurements are in millimeters; nm means the character could not be measured.

Specimen	Body	Antennal					Length of:			Ultimate			Tarsal		Setae on V	Antennal III	Longest Setae On:	Diameter of Sub-phuncular Cone
		III	IV	V	VI b	VI pt	Rostrum ^a	Rostral Segment ^b	Metatibia	I	II							
<i>Cinara louisianensis</i> Boudreaux																		
Apterac																		
07975-1b	1.67	.182	.096	.112	.099	.026	.80	.109 + .077 = .186	.84	.074	.218	.035-.093	.083	.125	.154			
07975-4b	2.07	.166	.070	.109	.122	.022	.83	.118 + .077 = .195	.81	.067	.211	.026-.067	.051	.083	.141			
07975-6tr	2.04	.186	.096	.122	.112	.022	.85	.128 + .083 = .211	.92	.077	.227	.048-.077	.080	.122	.134			
07975-7l	1.84	.179	.090	.122	.106	.022	.81	.118 + .077 = .195	.84	.067	.205	.032-.102	.080	.141	.147			
07975-9t	2.09	.186	.096	.115	.109	.022	.81	.125 + .080 = .205	.90	.074	.218	.032-.099	.086	.150	.144			
L-245-46 ^c	1.85	.171	.078	.114	.104	.018	1.07	.125 + .064 = .189	.79	.071	.207	.039-.061	.054	.090	.150			
L-245-46 ^c	1.89	.160	.102	.096	.102	.019	nm	.122 + .077 = .199	.77	.067	.202	.051-.074	.070	.096	.160			
Alatae																		
07975-2t	1.91	.208	.102	.115	.112	.019	.81	.096 + .080 = .176	.92	.067	.221	.070-.086	.112	.144	.128			
07975-4bl	2.40	.250	.115	.134	.122	.022	.86	.118 + .086 = .204	1.29	.077	.243	.086-.112	.115	.202	.160			
07975-8tl	1.96	.205	.109	.115	.115	.019	.78	.102 + .077 = .179	1.03	nm	.218	.058-.090	.106	.163	.102			
07975-8br	1.91	.192	.106	.119	.106	.019	.81	.102 + .080 = .182	1.01	.067	.221	.067-.109	.106	.179	.102			
07975-2b	1.92	.198	.096	.115	.112	.019	.82	.102 + .080 = .182	1.01	.074	.224	.074-.096	.093	.192	.096			
L-245-46 ^c	1.81	.218	.102	.115	.112	.022	.88	.102 + .077 = .179	1.05	.067	.205	.067-.096	.083	.173	.141			

Table 1. Continued.

Specimen	Length of:										Longest Setae On:		Diameter of Siphuncular Cone		
	Body	Antennal				Rostrum ^a	Ultimate		Tarsal		Setae on V	Antennal III		Metatibiae	
		III	IV	V	VI b		VI pt	Rostral Segment ^b	I	II					
<i>Cinara brevipilosa</i> Voeglin, Remaudière and Peña															
Apterae															
283-1 ^d	3.25	.403	.122	.179	.160	.060	1.85	.288 + .134 = .422	.163	.134	.298	<.009	.058	.064	.147
283-2	3.03	.422	.134	.186	.160	.064	1.89	.275 + .134 = .422	1.72	.134	.304	<.006	.048	.048	.154
283-3 ^{tr}	2.93	.416	.160	.198	.166	.070	1.82	.275 + .128 = .403	1.56	.125	.288	<.006	.061	.074	.141
283-3 ^{tl}	2.64	.384	.122	.160	.147	.058	1.76	.262 + .115 = .377	1.52	.125	.282	<.006	.048	.051	.128
283-8	3.19	.416	.147	.192	.160	.064	1.89	.282 + .134 = .416	1.61	.128	.294	<.009	.054	.058	.134
283-4	2.07	.230	.083	.141	.128	.070	1.61	.288 + .109 = .397	.86	.102	.243	<.009	.048	.045	.109
283-10	3.52	.410	.128	.186	.154	.064	1.94	.288 + .128 = .416	1.62	.134	.288	<.009	.064	.060	.160
283-7 ^l	3.19	.365	.134	.173	.141	.051	1.81	.262 + .128 = .390	1.52	.125	.262	<.009	.048	.058	.154
Alatae															
283-9 ^e	3.19	.454	.160	.198	.160	.064	1.89	.262 + .134 = .396	1.74	.122	.294	<.006	.054	.070	.154

^a Rostrum measurement is taken as defined by Bradley (1962).
^b Ultimate rostral segment used here and in text as a combination of segments IV and V.
^c Paratype specimens.
^d Holotype.
^e Morphotype.

the following: "Alate viviparae green; head dusky green; eyes black; ocelli black-bordered; antennae dusky black, with bases of segments paler; head powdery below; rostrum green, tinged with dusky, black at tip. Thorax dull green to dusky black, brown between lobes; coxae green, femora green at base, becoming dusky brown at apex; tibiae lightly infuscated, dark at tips; tarsi similar in color to tibiae. Abdomen dark green with transverse powdery areas behind cornicles; cornicles light brown; cauda and anal plate lightly infuscated."

Color of mounted specimen: As in apterae (Fig. 2B), but head more sclerotized, with lateral ocelli surrounded by a dark zone (Fig. 2C), antennal I, II distal $\frac{1}{3}$ of III, $\frac{1}{2}$ of IV and V, and $\frac{2}{3}$ of VI light brown (Fig. 2F), intersegmental scleroites more distinctly pigmented than in apterae; subgenital and spiracular plates darker than siphunculi; wings with subcostal vein and pterostigma dusky; joint area between femora and tibiae pale.

Morphology: Antennae with 1–3 secondary sensoria on III, (never 0, 1 in 9%, 2 in 68%, 3 in 23% of 68 antennae examined), 0–1 on IV (1 in 94%), 0–1 on V (1 in 50%); rostrum as in apterae but with lower ratio IV/V: 1.20–1.36. Internal side of lateral mesonotal lobes provided with an area slightly granulose, distinct in most sclerotized specimens. Media of fore wings poorly marked, with either 2 or 3 branches (in the latter, the 2nd fork is near the distal wing edge); among 24 specimens, 7 have 3–3 branches on their medias, 15 have 3–2 branches, and only 2 have 2–2 branches: of 48 wings examined, 40% have only 1 fork in the media.

Chaetotaxy: Similar to apterae, but setae a little longer and finer (less spine-like): longest setae on antennal III, 83–115 μm (Fig. 2F); on tibia III, 144–202 μm ; on tergite V, 86–112 μm ; on tergite VIII, 115–172 μm . Abdominal setae fewer than apterae: 19–24 on tergite V, 9–12 on tergite VIII, none standing on scleroites.

Measurements: Table 1.

First Instar Nymphs (described from 2 specimens).—Body length 1.0–1.1. Antennae 4 segmented (0.37–0.40); rostrum reaching the 5th abdominal tergite, about $\frac{1}{2}$ of the body length with ultimate rostral segment (0.20) 1.3 times longer than the 2nd joint of tarsus III and the ratio of IV/V = 1.5–1.6. Siphuncular cones pigmented, without setae, much lower than their basal diameter.

Chaetotaxy: Antennal segments bearing, respectively, 3 hairs on I and II, 10–12 on III, 5 on VI base, and 2 preapical setae on the conical process terminalis; vertex with about 8–9 pairs of strong setae (35–40 μm); rostral segment IV with 4 accessory setae. Dorsal abdominal setae distributed as follows: 2 spinal pairs of spine-like setae (20–45 μm), the longest ones on pigmented scleroites, accompanied with a few (0–3) shorter additional setae, and in the pleuro-marginal area 3–5 pairs of medium-sized setae; tergite VIII with 8–9 longer setae (90–100 μm) grouped on 2 slightly pigmented band-like sclerites. All 1st tarsal joints with 2 fine setae.

Diagnosis.—*Cinara louisianensis* and *C. tujaefilina* (del Guercio) are the only species feeding on Cupressaceae that have pale femorotibial joints. *C. tujaefilina* is larger than *C. louisianensis* (about 3 mm compared with about 2 mm) and is distinguishable by sclerotization and setae. Apterae of *C. tujaefilina* have 1 pair of sclerites on each thoracic segment; the apex of tibiae and tarsi, siphunculi, intersegmental scleroites, and paired sclerites on tergite VIII are quite dark; and alatae have the thorax and apex of femora very dark. Setal shape, length and number

(all are fine, never spine-like), are more numerous and longer than *C. louisianensis*. Additional characters for distinguishing between these two species are presented in Table 2.

Material examined.—Three paratype slides of *C. louisianensis*; 32 slides containing 14 apterae, 34 alatae and 11 nymphs taken on *Cupressus* sp., Mexico, D.F., 2230 m, Mexico, 3-IX-1982, A. L. Muñoz.

Discussion.—We have not been able to locate the holotype nor any specimens of the type series of *idahoensis*. Although Eastop and Hille Ris Lambers synonymized *louisianensis* with *idahoensis*, neither had seen any specimens of the Knowlton material (pers. comm., V. F. Eastop) and based their decision on measurements provided in the descriptions. We believe that *C. idahoensis* is not the same species as *C. louisianensis* for the following reasons. The illustrations in Knowlton (1935) seem to concern two distinct species: the antenna of the alate form (fig. 7) has only a few short setae on III and that of the apterous form (fig. 10) has many long setae on the same segment. Palmer (1952) examined a cotype aptera and wrote “indistinguishable from *winonkae*” (now considered a synonym of *tujafilina*), thus confirming the long antennal setae of this last form. Also, Knowlton’s (1935) description of *C. idahoensis* (“alate with cauda and anal plate blackish, apterous with cornicles dusky to black”) differs from that of *C. louisianensis* with its pale siphunculi, cauda and anal plate. Finally, Knowlton (1935) quoted for *idahoensis*, “0 secondary sensoria on antennal III of alatae.” In our 34 alatae of *louisianensis*, none have 0 sensoria on III and only 8 antennae have a single sensorium on this segment. The most common number was 2.

Cinara brevopilosa NEW SPECIES

Figs. 1C–D, 3

Apterous viviparous females (described from 14 specimens).—*Color in life*: No color notes made on living material.

Color of mounted specimens: Head medium to dark amber; antennal segments I, II and III slightly lighter than head, apex of (IV), V and whole of VI dark to almost black; rostrum with scleroites on the median part of II, apex of II and ultimate rostral segment dark to black. Pronotum uniformly sclerotized, mesonotum with 2 pairs of spinopleural sclerites, metanotum with a single pair; coxae, trochanters, proximal $\frac{1}{5}$ – $\frac{1}{3}$ of femora pale, apical part of femora gradually darker to tip; proximal joint of tibiae dark, then a pale region of approximately $\frac{1}{5}$ length followed by a gradual darkening to the tip which is as dark as the tarsus (Fig. 3A). Dorsum of abdomen, dominated by a large dark central sclerite (Fig. 3B) extending from tergite IV–VII and often joined to paired sclerites on III; this dorsal sclerite does not include the siphunculi nor the marginal area; tergite VIII with a sclerotized band extending laterally to the venter (Fig. 3E); subgenital plate incised anteriorly and posteriorly; abdomen with 4 pairs of black intersegmental scleroites ventrally.

Morphology: Antennae about $\frac{1}{3}$ – $\frac{2}{5}$ length of body; with 0 secondary sensoria on III, 0 on IV and 0–1 on V; satellite sensoria on VI not adpressed around the primary sensorium (Fig. 1C); rostrum 0.55–0.62 length of body (exceptionally .078 in a small specimen), ultimate rostral segment 1.3–1.7 times the 2nd metatarsus, ratio IV/V = 1.9–2.6 (Fig. 1D). Mesosternum without tubercle. Siphuncular cones short (Fig. 3F). Cauda broadly rounded (Fig. 3B).

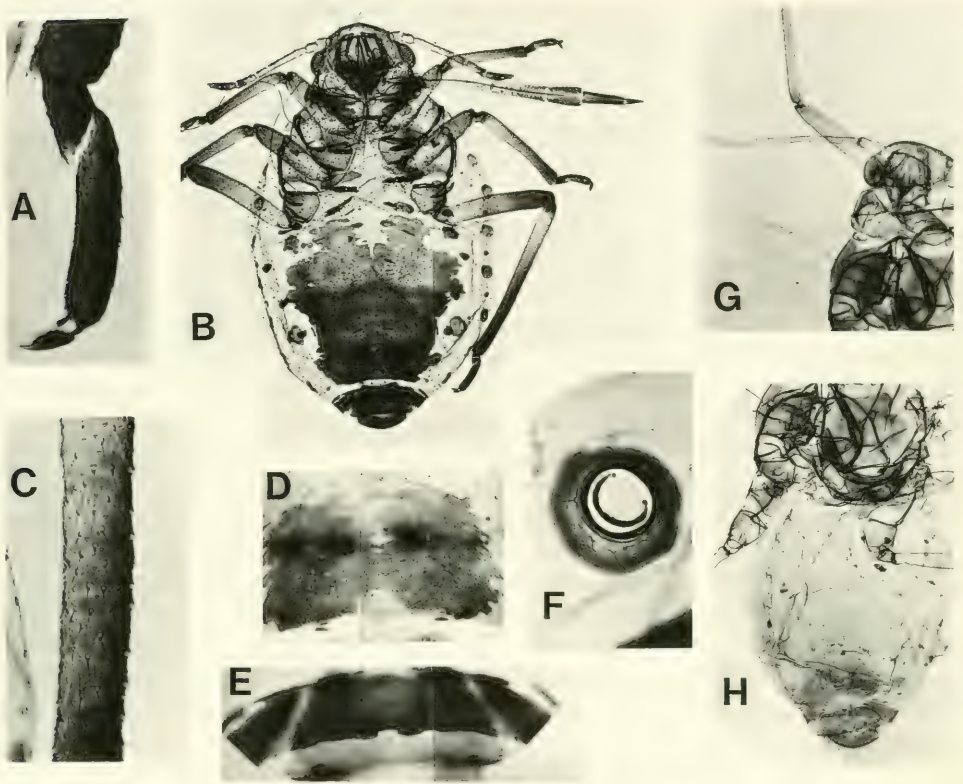


Fig. 3. *Cinara brevopilosa*. A, First and second segments of metatarsus of aptera. B, Apterous viviparous female showing extensive sclerotic plate on dorsum of abdomen. C, Section of metatibia of aptera. D, Subgenital plate of aptera. E, Wide sclerotized band on tergite eight of aptera. G, Head and antenna of alate. H, Pterothorax and abdomen of alate. Photography by G. Remaudière.

Chaetotaxy: Antennae with 8–12 setae on II, 22–29 on base of VI and 6–8 preapical setae on process terminalis (one with 3); rostral segment IV with 11–15 accessory setae (often 7 pairs) along sides of stylet groove (Fig. 1D); dorso-cephalic setae very short (7–8 μm) and with parallel sides. Dorsal setae on thorax and abdomen I–VIII short or shorter than on head, those located on membranous areas are each on a small pigmented scleroite; tergite V with 41–54 setae; si-phuncular setae fine but rarely exceeding 40 μm , scattered over the upper half of cone, in some specimens some additional very short setae are located on base of cones; tergite VIII with 26–35 setae, those of the center short (15–20 μm), lateral ones longer (up to 80 μm) and finer, subgenital plate with 90–100 setae (Fig. 2E) (one specimen with 66); ventral abdominal setae long (55–70 μm) with acute tip. Setae on tibiae are at 30–60 degrees, similar all around the tibiae and shorter (60–70 μm) than diameter of tibia, with a very fine and hardly distinguishable apex (Fig. 3C).

Measurements: Table 1.

Alate viviparous female (described from one specimen).—*Color of mounted specimen*: Figs. 3G, H. The single available specimen appears slightly teneral.

Table 2. A comparison between *C. louisianensis* and *C. tujafilina*, the only two species feeding on Cupressaceae that have pale femortibial joints.

	Apterae		Alatae	
	<i>C. louisianensis</i>	<i>C. tujafilina</i> ^a	<i>C. louisianensis</i>	<i>C. tujafilina</i> ^a
Number of setae on:				
Antennal segm. VIb	4-6	8-14	4-6	9-13
Process terminalis (subapical)	(1) 2	3	(1) 2	(3) 4
IVth rostral segm. (accessory)	4	5-8	3-5	4-8
Abd. tergite V	24-36	50-70	19-24	38-60
Abd. tergite VIII	8-13	19-26	9-12	17-24
Maximum length of setae on:				
Antennal segm. III	.051-.086	.120-.140	.093-.115	.130-.160
Abd. tergite V	.061-.102	.100-.150	.086-.121	.140-.180
Abd. tergite VIII	.140-.140	.150-.190	.115-.172	.160-.200
Ratio rostral segm. IV/V	1.40-1.58	1.80-2.00	1.20-1.36	1.65-1.85
Secondary sensoria on:				
Antennal segm. III	0	0	1-3 (4)	2-8
Antennal segm. IV	0	(0) 1-2 (3)	(0) 1	1-2
Antennal segm. V	0-1	(0) 1 (2)	0-1	(0) 1

^a Data for *C. tujafilina* taken from Eastop (1972).

Head and pterothorax dark, prothorax lighter. Abdomen lacking large central sclerite of apterae, only tergite VII with irregularly shaped sclerites (Fig. 3H); tergite VIII with sclerotic band extending laterally to venter as in apterae. Siphuncular cones and appendages patterned as in apterae.

Morphology and Chaetotaxy: Antennae with 5-7 secondary sensoria on III, 0 on IV and V. All dorso-abdominal setae with very small sclerites at their base. Subgenital plate with over 100 setae evenly distributed over the entire plate. Other characters similar to those described for apterae.

Measurements: Table 1.

Diagnosis.—Three other species of *Cinara* in North America have a large dorsal sclerite on the abdomen: *Cinara osborni* Knowlton (1942), which lives on *Pseudotsuga menziesii* (Mirb.) Franco; *Cinara canatra* Hottes and Bradley (1953), on *Pinus contorta* Dougl. ex Loud. and *P. banksiana* Lamb; and *Cinara glabra* Gillette and Palmer (1924), on *Pinus ponderosa* Dougl. ex P. & C. Lawson.

Cinara osborni has the entire dorsum sclerotized including the siphuncular cones (not included in *brevipilosa*); ultimate rostral segment much shorter (0.7) than 2nd metatarsus (much longer 1.3-1.7 in *brevipilosa*); siphuncular cones bearing some long setae interspersed with more numerous short, fine setae (only a few fine setae in *brevipilosa*); body setae abundant and long, 80-95 μm against 6-10 μm in *brevipilosa*.

Cinara canatra also has the siphuncular cones included in a large sclerite which is less extensive than the sclerite in *osborni*.

In *glabra*, the dorsal abdominal sclerite does not include the siphuncular cones but is usually wider than in *brevipilosa*, extending laterally past the muscle attachment plates, whereas the sclerite in *brevipilosa* is limited to the region delin-

eated by the muscle attachment plates (Fig. 2B). The two species are very similar morphologically. Using the key to *Cinara* in Palmer (1952), *brevipilosa* runs to *glabra*. Besides their different extension of the dorsal shield, the two *Cinara* can be easily discriminated by setal density as follows. Numbers for *brevipilosa* followed by those for *glabra*. Number of setae on: base of antenna VI 22–29, 11–13; process terminalis (3) 6–8, 4–6; antennal II (8) 10–12, 6–9; .2 mm mid hind tibia 61–79, 30–40; tergite V 41–50, 24–34; subgenital plate (66) 93–108, 49–64; siphuncular cones 11–17, 13–27.

In most cases *brevipilosa* has more setae, except on the process terminalis and the siphuncular cones. The slightly larger sclerotized area of the siphuncular cones of *glabra* makes this difference.

Types.—Holotype apterous viviparous female on slide #283-1. Morphotype, alate viviparous female, slide 283-9. Paratypes, 14 apterous viviparae. Collection #283 taken by R. Peña/García Calderon on *Pinus* sp., Timgambato, Michoacan, Mexico, 21-X-1981. Holotype deposited at the Illinois Natural History Survey. Paratypes are distributed in the collections of the coauthors' respective institutions and in the National Museum of Natural History (Washington), Canadian National Collection (Ottawa) and British Museum of Natural History (London).

Etymology.—The name is based on the very short dorsal abdominal setae.

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**A HORNET, PAPER WASPS, AND YELLOWJACKETS
(HYMENOPTERA: VESPIDAE) IN SUBURBAN HABITATS
OF THE WASHINGTON, D.C., AREA**

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Abstract. —Based on Malaise trap catches made in five suburban habitats during 1980 to 1984, 1 hornet (*Vespa*), 2 paper-wasp (*Polistes*), and 9 yellowjacket (*Dolichovespula*, *Vespula*) species were found in the Washington, D.C., area: *Dolichovespula arenaria*, *D. maculata*, *Polistes exclamans*, *P. fuscatus*, *Vespa crabro*, *Vespula acadica*, *V. flavopilosa*, *V. germanica*, *V. maculifrons*, *V. squamosa*, *V. vidua*, and *V. vulgaris*. *Vespula maculifrons* was the most frequently captured species. *Vespula acadica* has not been previously reported in the study area. Traps were used for 2 to 5 years in each location, and they each caught eight to 10 species. Their catches were often significantly correlated with regard to species and species abundances; nonetheless, cases of no correlation suggest marked catch differences among traps. Walk counts and Malaise trap counts made in the same habitat during the same week often produced different indications of species composition and abundances.

This study has three aims. First, it reports the species of paper wasps (*Polistes*), yellowjackets (*Dolichovespula*, *Vespula*), and hornet (*Vespa*) found, their relative abundances, and their flight times in five suburban habitats in the Washington, D.C., area. Four of the habitats were in Maryland: a highly disturbed yard garden, a wooded-stream habitat, a periodically mowed field, and the ecotone between the wooded-stream habitat and a lawn. The fifth site was a residential yard in Virginia. The study data were obtained from Malaise traps. Second, this investigation describes how catches differ among the traps. Last, it compares wasp abundance determinations based on contemporaneous walk counts with Malaise-trap catches in the yard garden.

Paper wasps, yellowjackets, and hornets are primitively eusocial wasps that are often common in temperate, suburban habitats. These wasps are beneficial predators that consume pestiferous insects, such as lepidopterans that eat crops, and, thus, have been studied as possible biocontrol agents in the U.S. (Gillaspay, 1977; Gould and Jeanne, 1984). Further, they scavenge wastes, and thereby help to recycle environmental resources. However, these wasps are often considered to be pests because they have potent stings and nest near, on, or in houses and other buildings; and some species are nuisances when they are attracted to food at picnics, in garbage cans, and other places (Davis, 1978; Akre et al., 1981; pers. obs.).

In North America, previous investigators have studied many aspects of the

biologies of these wasps (Akre et al., 1981). For example, Matthews (1982) investigated seasonal abundances of queens of *Vespula maculifrons* and *V. squamosa* based on walk and Malaise-trap counts in three Georgia suburban habitats. Roush and Akre (1978) used heptyl-butyrate traps and Malaise traps to study seasonal abundances of *Dolichovespula* and *Vespula* in Oregon. However, the seasonal cycles and flight periods of the paper wasps, yellowjackets, and hornet have not been previously elucidated in the Washington, D.C., area.

In this area, I found that six Malaise traps used from April to mid-November 1980–1984, collected 12 species of these wasps. All traps obtained similar numbers of species, but species abundances were significantly correlated between only some of the traps. Walk counts were often uncorrelated with contemporaneous trap counts from the same habitat.

MATERIALS AND METHODS

This study used five Cornell-style and one Townes-style Malaise traps. The pyramidal, 2-m-tall Cornell traps are made of white gauze and aluminum-pipe supports. The bases of the traps are 1.2×1.2 m, and each of their four sides has a rectangular arthropod-catching opening of 0.8-m^2 that extends from the ground to 70 cm above it. David R. Smith, who donated data to my study, trapped wasps using the Townes trap, which has two black-gauze, 1.8-m^2 , rectangular catching surfaces extending from the ground to 1.1 m above it. The remainder of the gauze of his trap is white.

All traps were left up 24 h per day from 1 April to mid-November. Wasp species and their abundances were determined from catches obtained from 1 April to 31 October. Late flight times were obtained from the November catches. Captured insects were removed from traps approximately once per week.

All traps were within 15 km of Washington, D.C. Smith trapped wasps in the yard of his residence near Annandale, Fairfax County, Virginia. His trap was shaded by *Acer saccharinum* L., *Pinus strobus* L., and *Malus* sp.

I used two Cornell traps in my yard garden in Glen Echo, Maryland, and one in a wooded-stream habitat, field, and the ecotone between the wooded-stream habitat and a lawn in the David W. Taylor Naval Ship Research Center, 5 km NNW of Glen Echo. I chose this Center because it was a safe place where I could trap wasps in habitats that are more natural than suburban yards. The Center is fenced and guarded 24 h per day. In past work, three of my traps in unprotected sites were cut up, torn, or both by vandals.

In the yard garden, I placed one trap (the south trap) 0.3 m from the southwest corner of my house from 1982 to 1984 and a second trap (the north trap) 1 m from the northeast corner of my house from 1980 to 1984. The south trap was unshaded by trees or houses, while the north trap was usually in shade from houses, *Acer negundo* L. and *Pinus strobus*. I regularly watered my yard garden during dry spells making it one of the moister and floriferous areas in Glen Echo. It attracted wasps because it usually contained flowers that they used as nectar sources, including *Asclepias curassavica* L., *Celosea argentea* L., *Helianthus cvs.*, *Impatiens balsamina* L., and *Pastinaca sativa* L., and during dry spells, wasps drank from water droplets on plants. Nests of *Polistes exclamans* and *Dolichovespula maculifrons* occasionally occurred in my yard garden.

At the Taylor Research Center, the wooded-stream habitat contained large trees

including *Quercus* spp., *Liriodendron tulipifera* L., and *Platanus occidentalis* L. The ecotone was an irregular edge of this woods and a 1-m-wide strip of low brush that ran east and west and was bordered by lawn on its south side. The ecotone trap was placed near a lawn instead of next to the field because there was no available east-west edge of the woods adjacent to the field. The ecotone trap was in direct sunlight during afternoons and the field trap was in direct sunlight all day. Grasses dominated the field which was mowed once in 1983 (September) and once in 1984 (June).

Cornell trap catches were reduced by certain arthropod activities within the traps including the following. Carpenter bees (*Xylocopa virginica* L.) periodically bit holes in their gauzes just below their collecting heads, and they, as well as other arthropods, escaped through the holes until I repaired them with silicone glue and gauze patches. I saw a few carpenter bees and bumble bees crawl down trap sides and escape through usual openings. Occasional spiders and praying mantids perched inside traps just below collecting heads where they consumed ample prey until I found these predators and removed them. Finally, large butterflies, which did not crawl into the funnel of the catching head, remained just below it until I removed them or they fell to the ground dead or in feeble states.

Contemporaneous trap catches and walk censuses were made in July–August, 1983. I made one walk count per day between 11 a.m. and 5 p.m., 3–7 days per week.

Possible correlations in the numbers of individuals of the 12 captured wasp species between traps were analyzed using the Spearman-rank-correlation-coefficient program of the SAS computer package (Ray 1982a, b). Voucher specimens were deposited in the U.S. National Museum (U.S.N.M.).

RESULTS AND DISCUSSION

Species richness and relative abundances.—The 12 species of captured wasps and their feeding behaviors (based on Barrows, 1979, pers. obs.; Akre et al., 1981; MacDonald and Matthews, 1984) are: *Dolichovespula arenaria* (Fabricius), predator, carrion scavenger; *D. maculata* (L.), predator, protein scavenger; *Polistes exclamans* Viereck, predator, nectar forager; *P. fuscatus* (Fabricius), predator, nectar and honey-dew forager; *Vespa crabro* L., predator, plant-sap forager; *V. acadica* (Sladen), predator; *V. flavopilosa* Jacobson, feeding behavior unknown; *V. germanica* (Fabricius), predator, protein scavenger and sugar forager; *V. maculifrons* (Buysson), predator, scavenger; *Vespula squamosa* (Drury), social parasitism of host's food, protein scavenger; *V. vidua* (Saussure), predator?; and *V. vulgaris* (L.), predator, protein scavenger and sugar forager. "Predator" indicates being a predator of insects.

The numbers of individuals of each species collected are listed in Table 1. Counts for each wasp species are the total numbers of queens, workers, and males obtained in all 5 yr of the study. Traps collected similar numbers (8–10) of wasp species even though two kinds of traps were used, and trap locations were so different. The field trap collected the largest annual number of wasps, followed, in decreasing order, by the yard-garden south trap, yard trap, ecotone trap, yard-garden north trap, and wooded-stream-habitat trap.

Vespula maculifrons was the most frequently obtained species, followed in decreasing order by *Polistes fuscatus*, *Dolichovespula maculata*, *Polistes exclamans*.

Table 1. Numbers of wasps of each species collected in suburban habitats. Wasps: DA, *Dolichovespula arenaria*; DM, *D. maculata*; PE, *Polistes exclamans*; PF, *P. fuscatus*; VA, *Vespula acadica*; VC, *Vespa crabro*; VF, *Vespula flavopilosa*; VG, *V. germanica*; VM, *V. maculifrons*; VS, *V. squamosa*; VV, *V. vidua*; VVu, *V. vulgaris*. Traps: ET, ecotone; FT, field; YGNT, yard-garden north; YGST, yard-garden south; YT, yard; WSHT, wooded-stream-habitat. N, number of species taken by a particular trap; WPY, mean number of wasps collected per trap per year.

Trap and Years	Species												N	WPY
	DA	DM	PE	PF	VA	VC	VF	VG	VM	VS	VV	VVu		
YGNT														
1980-1984	2	2	31	219	0	0	0	2	145	1	2	1	9	81
YGST														
1982-1984	1	3	23	147	0	5	0	6	100	1	0	0	8	95
YT														
1982-1984	6	35	0	59	0	1	3	2	149	0	1	2	9	86
WSHT														
1983-1984	20	8	0	2	0	5	0	2	42	1	5	3	9	44
ET														
1983-1984	11	25	0	58	1	8	0	1	53	0	0	10	8	84
FT														
1983-1984	5	7	3	77	0	3	0	1	121	1	1	2	10	111
Total	45	80	57	562	1	22	3	14	610	4	9	18	—	—
Abundance														
Rank	5	3	4	2	12	6	11	8	1	10	9	7	—	—

mans, *Dolichovespula arenaria*, *Vespa crabro*, *Vespula vulgaris*, *V. germanica*, *V. vidua*, *V. squamosa*, *V. flavopilosa*, and *V. acadica*. The ecotone trap collected one worker of *Vespula acadica*, a species not previously found in the Washington, D.C., area according to a distribution map in Akre et al. (1981). Maps in this reference also suggest that *Dolichovespula arctica* and *Vespula consobrina* occur in the Washington, D.C., area; however, the traps did not obtain them. Further, I did not find any specimens of any of these three species and *V. flavopilosa* from the Washington, D.C., area in the U.S.N.M. collection. Although specimens for *Polistes annularis* from this area were found in the U.S.N.M. collection, none were collected by the traps. However, they did obtain all species of *Vespula*, *Vespa*, and *Dolichovespula* found in the U.S.N.M. collection for the Washington, D.C., area.

Comparisons of trap catches.—Fifteen correlation analyses of the number of individuals of each of the 12 species collected by individual traps were performed (Table 2). The field trap was positively correlated with all other traps; the ecotone trap catch was correlated with all traps except the yard-garden ones; the yard-garden traps were correlated with each other and the field trap; the wooded-stream-habitat trap was correlated with all but the yard-garden traps; and the yard trap was correlated with all but the yard-garden traps. Thus, the data suggest that the field trap collected a species group with relative abundances intermediate between those of yard-garden traps and the rest of the traps.

Flight times.—Flight periods of wasps are listed in Table 3. When queens could

Table 2. Significance levels (Ps) of Spearman-rank correlation coefficients resulting from comparisons of the number of individuals in each of 12 species caught by each of six traps during all years that it was used. The abbreviations for traps are the same as those used in Table 1. Nonsignificant Ps ($P > 0.05$) are enclosed by parentheses.

	FT	WSHT	YGNT	YGST	YT
ET	0.0017	0.0268	(0.1327)	(0.1022)	0.0023
FT		0.0149	0.0071	0.0064	0.0172
WSHT			(0.2669)	(0.5034)	0.0329
YGNT				0.0067	(0.0957)
YGST					(0.2065)

be easily distinguished by their large sizes compared to workers, flight seasons of both queens and workers are listed separately. Matthews (1982) reported flight times for queens of *V. maculifrons* and *V. squamosa*, based on Malaise-trap and horse-fly trap catches in Athens, Georgia, that are earlier than the ones that I found, possibly a result of an earlier spring in Athens. Based on heptyl-butyrate and modified-Malaise-trap counts in 1977 in Oregon, Roush and Akre (1978) found the first workers of species, common to both Oregon and the Washington, D.C., area, on dates similar to mine: *D. arenaria*, 5 June; *D. maculata*, 7 July; and *V. vulgaris*, 6 July.

Walk vs. Malaise-trap censuses.—Comparisons of walk and Malaise-trap censuses in the yard garden (Table 4) indicate that these methods yield markedly

Table 3. Flight times of collected wasps from all years and traps combined. The years in which the earliest, latest specimens, or only specimens were trapped are given in parentheses.

Species	Flight Periods
<i>Dolichovespula arenaria</i>	males, 15 July–30 September (1984); workers, 12 June (1983)–4 November (1984)
<i>D. maculata</i>	males, 5 November (1981); queens, 14–31 May (1984), 11–15 October (1984); workers, 8 July–11 September (1983)
<i>Polistes exclamans</i>	females, 8 April (1984)–21 August (1983)
<i>P. fuscatus</i>	females, 4 April (1981)–1 November (1983)
<i>Vespa crabro</i>	queens, 15 May (1983), 7 August–2 October (1983); workers, 3 July (1983)–25 October (1984)
<i>Vespula acadica</i>	worker, 21 August (1983)
<i>V. flavopilosa</i>	male, 30 September (1984); workers, 5 August–4 November (1984)
<i>V. germanica</i>	queens, 20 April–6 May (1982), 1 November (1983); workers, 25 July (1982)–21 October (1981)
<i>V. maculifrons</i>	males, 21 October–5 November (1981); queens, 9 April (1981)–26 June (1983); workers, 17 June (1981)–9 November (1980)
<i>V. squamosa</i>	queens, 31 May–20 June (1984); workers, 7 August–21 August (1983)
<i>V. vidua</i>	queens, 14 May–12 June (1984); workers, 12 July (1984)
<i>V. vulgaris</i>	males, 21 August (1983); queens, 24 April (1980)–24 July (1983); workers, 15 July (1984)–2 October (1983)

Table 4. Per-day counts of wasps from walk censuses and trap censuses made in the yard garden in 1983. For each week, the number of days on which I made walk censuses is indicated in parentheses. T, trap census; W, walk census.

Species	Weeks									
	July		August							
	25-31 (4)		1-7 (4)		8-14 (3)		15-21 (7)		September	
	T	W	T	W	T	W	T	W	T	W
<i>Dolichovespula maculata</i>	0.3	0.5	0.4	0.3	0	0.3	0	0.6	0	0
<i>Polistes exclamans</i>	0.3	2.0	0.1	1.0	0.1	1.0	0.3	0.1	0	0.3
<i>P. fuscatus</i>	1.6	7.0	1.3	5.3	0.3	4.3	0.4	2.4	0	1.3
<i>Vespa crabro</i>	0	0	0.3	0	0	0	0	0	0	0
<i>Vespula germanica</i>	0	0	0	0	0	0	0.1	0	0	0
<i>V. maculifrons</i>	0.3	0.3	0.1	0	0.6	0	0.4	0.3	0	0
<i>V. squamosa</i>	0	0	0.1	0	0	0	0.4	0.1	0	0
<i>V. vulgaris</i>	0	0	0	0	0	0	0	0.1	0	0

different results when simultaneously used to sample wasps. Walk censuses found five species that the trap did not collect during the same weeks, but trap censuses found five species that the walk censuses did not reveal, and in 22 of the 40 comparisons, walk and trap censuses were not identical. Nonetheless, one type of sampling alone is likely to give a reasonable indication of relative population size changes of particular species that it commonly censuses (Roush and Akre, 1978). Because no species of wasps in the studied genera were seen during any walk censuses in the yard garden that were not caught by the traps, the traps alone were an adequate means of sampling species richness of these genera.

The type and location of a Malaise trap affects what species and how many of them that it catches (Matthews and Matthews, 1970). In my study, even two close-by traps in the yard garden caught markedly different numbers of some species, and they even caught different species (Table 1). Matthews and Matthews (1970) indicate that Townes traps catch many more arthropods than Cornell traps. Nonetheless, in my study, the Townes trap caught only the third-highest number of wasps, and it did not collect the largest number of species. This might be due to its location, which was shaded and not immediately adjacent to many nectariferous flowers for much of the flight season, rather than its catching ability.

In conclusion, the Malaise traps caught 12 vespine species in *Dolichovespula*, *Polistes*, *Vespa*, and *Vespula* in five suburban-area habitats. During 5 years, hundreds of wasps were obtained, with trap designs and locations evidently affecting the numbers of individuals of the different species that were captured. Because contemporaneous walk censuses and trap captures gave different indications of the numbers and abundances of species, a combination of sampling methods is probably needed to give a complete picture of vespine-wasp community structure of a sampled region.

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A REVISION OF THE NEARCTIC SPECIES OF THE GENUS
ZAOMMOMYIA ASHMEAD (HYMENOPTERA, EULOPHIDAE)

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Abstract.—The nearctic species of the genus *Zaommomyia* Ashmead are revised. Two new species, *Z. minuta* and *Z. sulciscuta* are described. Two additional species, *Chrysocharis beckeri* Yoshimoto and *Gastrancistrus vonones* Walker are transferred to *Zaommomyia*. *Derostenus acutus* Ashmead, *Sympiesis grenadensis* Howard and *Chrysocharis majoriani* are new synonyms of *Z. vonones* (Walker). Lectotypes are designated for *S. grenadensis* Howard, *C. majoriani* Girault and *Chrysocharis stigmata* Ashmead. *Zaommomyia* has its main distribution in the Neotropical Region, and nearctic species are mainly found in the southern parts of the Region. Hosts are known only for one species, *Z. vonones*, a parasitoid of *Agromyzidae* (Diptera).

When Ashmead (1904) described *Zaommomyia*, he diagnosed the genus in a key where he included all neotropical genera of his tribe Omphalini. A thorough description was never presented and the genus has never been treated taxonomically or otherwise since it was described. According to the original diagnosis *Zaommomyia* was similar to *Chrysocharis* Förster, differing mainly in having a very narrow malar space, "malar space wanting."

Zaommomyia is similar to *Chrysocharis*, the main differences being in the appearance of the frons and the antennae. The diagnostic character used by Ashmead, a narrow malar space in *Zaommomyia*, is based on an artifact. The type specimen of *Chrysocharis stigmata* Ashmead, which is the type species of *Zaommomyia*, has the lower part of the compound eyes disrupted and the malar space appears very narrow. I have, however, seen intact specimens conspecific with *stigmata* and the malar space is quite wide (as in Figs. 1, 2). Males of *Zaommomyia* have verticillate setae on flagellar segments (Figs. 8, 11), i.e. with projecting setae concentrated to the basal half of each segment, in nearctic species usually in two rows. Females have conspicuously long ventral setae on flagellar segments (Figs. 7, 9, 10). The appearance of the frons in *Zaommomyia* (Figs. 1, 2) is quite unlike that of *Chrysocharis* (Fig. 14). In *Zaommomyia* the antennal scrobes never meet as in *Chrysocharis*, and the lower part of the frons above the fork is flattened in *Zaommomyia*, a feature never seen in *Chrysocharis*. The appearance of the frons is similar in both sexes in *Zaommomyia*; in *Chrysocharis* there are usually pronounced differences between the sexes in this character. Nearctic species of *Zaommomyia* always have a narrow costal cell and tridentate mandibles. These characters are, however, present in some *Chrysocharis* species and are not diagnostic

for *Zaommomyia*. Otherwise, *Zaommomyia* is similar to *Chrysocharis* (diagnosis in Hansson, 1985).

Zaommomyia appears to be most diverse and widespread in the Neotropical Region. The nearctic species are mainly found in the southern parts of the Region, except for *Z. beckeri* which reaches as far north as southern parts of Quebec (Gatineau Park). Hosts are known only for *Z. vonones*, a parasitoid of leafmining Agromyzidae (Diptera).

Morphological terms used are explained in Hansson (1985), the exception being POO, the distance between posterior edge of hind ocelli and occipital margin. Abbreviations of museums and private collections used in the text were as follows; BMNH = British Museum (Natural History), London, England; CH = collection of author; CNC = Canadian National Collections, Ottawa, Canada; LUZM = Lund University Zoological Museum, Sweden; USNM = National Museum of Natural History, Washington, D.C., USA.

Genus *Zaommomyia* Ashmead

Zaommomyia Ashmead, 1904: 340. Type-species: *Chrysocharis stigmata* Ashmead, 1894: 175, by original designation.

I have examined the lectotype (present designation) of *Chrysocharis stigmata*, a ♂ in BMNH labelled “St. Vincent, W.I. H. H. Smith,” “W. Indies 99-331,” “Type,” “*Chrysocharis stigmatius* Ashm. ♂ Type,” “B.M. Type Hym. 5.1324,” “*Zaommomyia stigmata* (Ashm.) det. Z. Bouček 1975.” This species was described from the West Indies. It differs from known nearctic species in having the following combination of characters: forewing with setae on marginal fringe 2× as long as in Fig. 3, speculum closed, with a fuscous spot below stigmal vein, coxae dark and metallic, propodeum with a complete carina between petiolar foramen and spiracular sulcus (as in Fig. 4) and petiole dark.

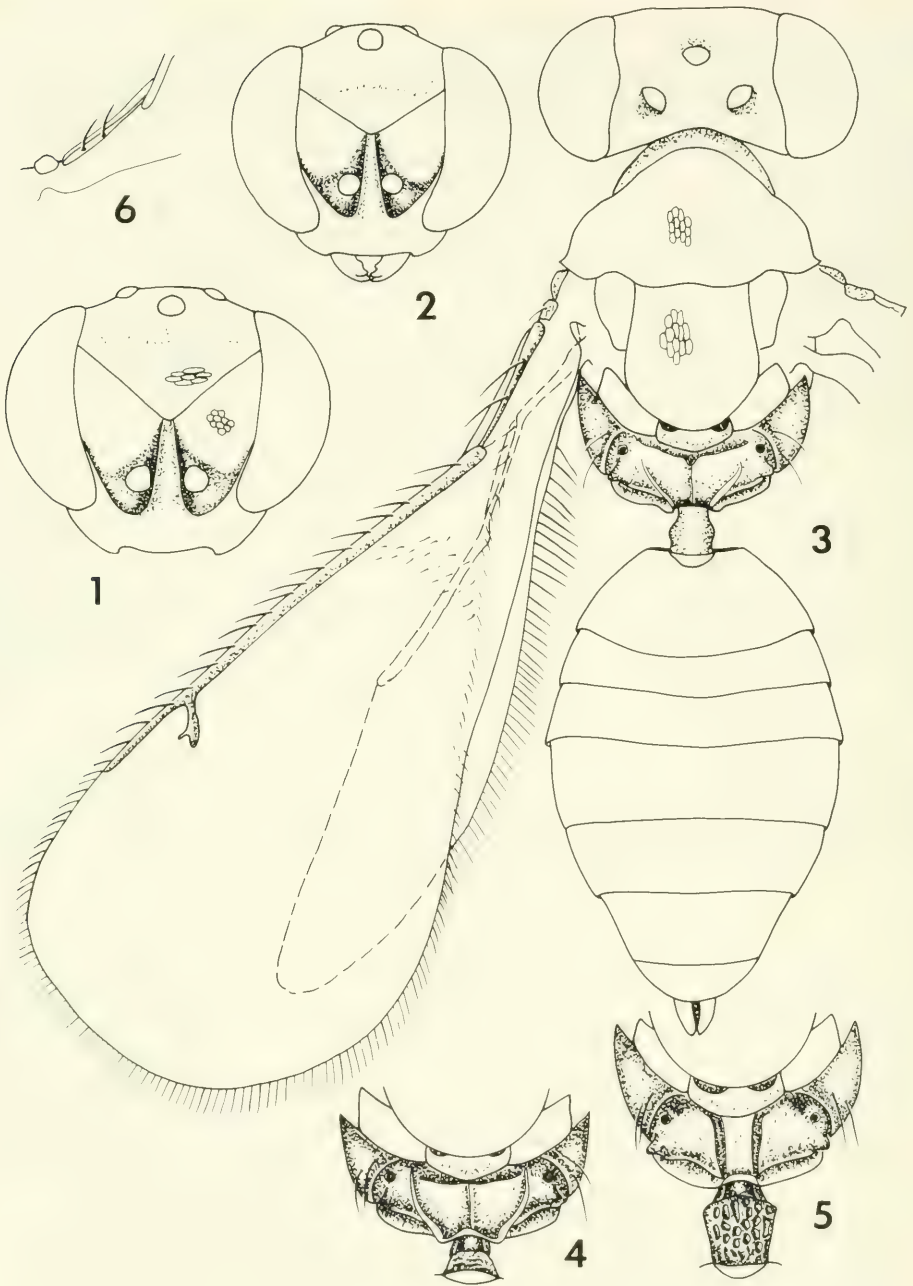
KEY TO THE NEARCTIC SPECIES OF *ZAOMMOMYIA*

1. Propodeum with two complete parallel submedian grooves, petiole 1.5× as long as wide, with strong sculpture (Fig. 5) *Z. sulcata* new species
- Propodeum never with such grooves, petiole at most as long as wide, smooth or with very weak sculpture 2
2. Petiolus dark and metallic, raised surface consisting of a transverse and narrow strip (Fig. 4), speculum of forewing open *Z. vonones* (Walker)
- Petiolus pale, as long as wide and smooth, speculum of forewing closed 3
3. Horizontal arms of frontal fork almost straight, thoracic dorsum with fine, weak reticulation *Z. minuta* new species
- Horizontal arms of frontal fork V-shaped (Fig. 2), thoracic dorsum usually with strong reticulation *Z. beckeri* (Yoshimoto)

Zaommomyia vonones (Walker)

Figs. 1, 4, 7, 8

Gastrancistrus vonones Walker, 1839: 67, **NEW COMBINATION**.
Derostenus acutus Ashmead, 1894: 174, **New Synonymy**.
Sympiesis grenadensis Howard, 1897: 163, **New Synonymy**.



Figs. 1-6. *Zaommomyia* spp. 1, *Z. vonones* (Wlk.) ♀, head, front view. 2-3, *Z. beckeri* (Yshm.) ♀. 2, Head, front view. 3, ♀ habitus. 4, *Z. vonones* ♀, dorsellum + propodeum + petiolus, dorsal view. 5-6, *Z. sulcata* n. sp. 5, ♀, dorsellum + propodeum + petiolus, dorsal view. 6, Base of right fore wing. Scale = 0.25 mm for antennae, 0.50 mm for remaining illustrations.

Pediobius grenadensis (Howard), transferred by Ashmead, 1900: 263.

Chrysocharodes majoriani Girault, 1917: 10, **New Synonymy**.

Chrysocharis majoriani (Girault), transferred by Burks in Krombein & Burks, 1967: 232.

Chrysocharis vonones (Walker), transferred by Graham, 1969: 851.

Chrysocharis acuta (Ashmead), transferred by Bouček, 1977: 4.

Achrysocharella acutus (Ashmead), transferred by deSantis, 1979: 279.

Diagnosis.—Mid- and hindcoxae completely pale (♀), speculum open, propodeum usually with complete carinae between petiolar foramen and spiracular sulcus, petiole dark and metallic with raised surface consisting of a transverse and narrow strip.

Description.—*Female*: Length of body: 1.4–1.5 mm. Head: Scape pale, remainder of antenna dark. Flagellum with three apical segments more fused than basal two, segments I and III about $1.9\times$, II and IV $2.2\text{--}2.4\times$, and V about $4.1\times$ as long as wide. Face and clypeus golden-purple. Ratios height of eye/malar space/mouth opening; $3.9/1.0/1.9$. Malar space $1.5\times$ as wide as width of scape. Frons below fork golden-purple, reticulation with quite high and quite narrow—quite wide septa, with small meshes. Frontal fork Y-shaped. Lower triangle on frons above fork with same color and reticulation as below fork, meshes transversely elongate, remaining parts of frons above fork and vertex golden green, reticulate with very low and very narrow septa, or smooth. Inner orbit of compound eye with one row of setae. Ratios POL/OOL/POO; $2.7/1.4/1.0$. Occipital margin rounded. Ratio width of head/width of thorax across shoulders; 1.20.

Thorax (including propodeum): Pronotal collar without transverse carina. Mesoscutum and scutellum golden green, reticulation with quite high and quite wide septae. Dorsellum flat, smooth and shiny. Borderline between lower and upper epimeron almost straight. Forecoxa pale—dark and metallic, mid- and hindcoxae pale. Remaining parts of legs pale. Wings hyaline, forewing rounded with speculum open. Ratios length of marginal-/postmarginal-/stigmatal veins; $8.9/2.3/1.0$. Propodeum with same color as thorax, anteromedian part with or without a very short but wide fovea, usually with complete carinae between petiolar foramen and spiracular sulci, median carina complete, and median part with or without reticulation. Propodeal callus with 2 setae. Petiolar foramen rounded triangular.

Petiole: Small, raised surface forming a transverse and narrow strip, dark and metallic.

Gaster: Oval, ratio length of thorax + propodeum/length of gaster; $0.83\text{--}0.91$, $n = 4$.

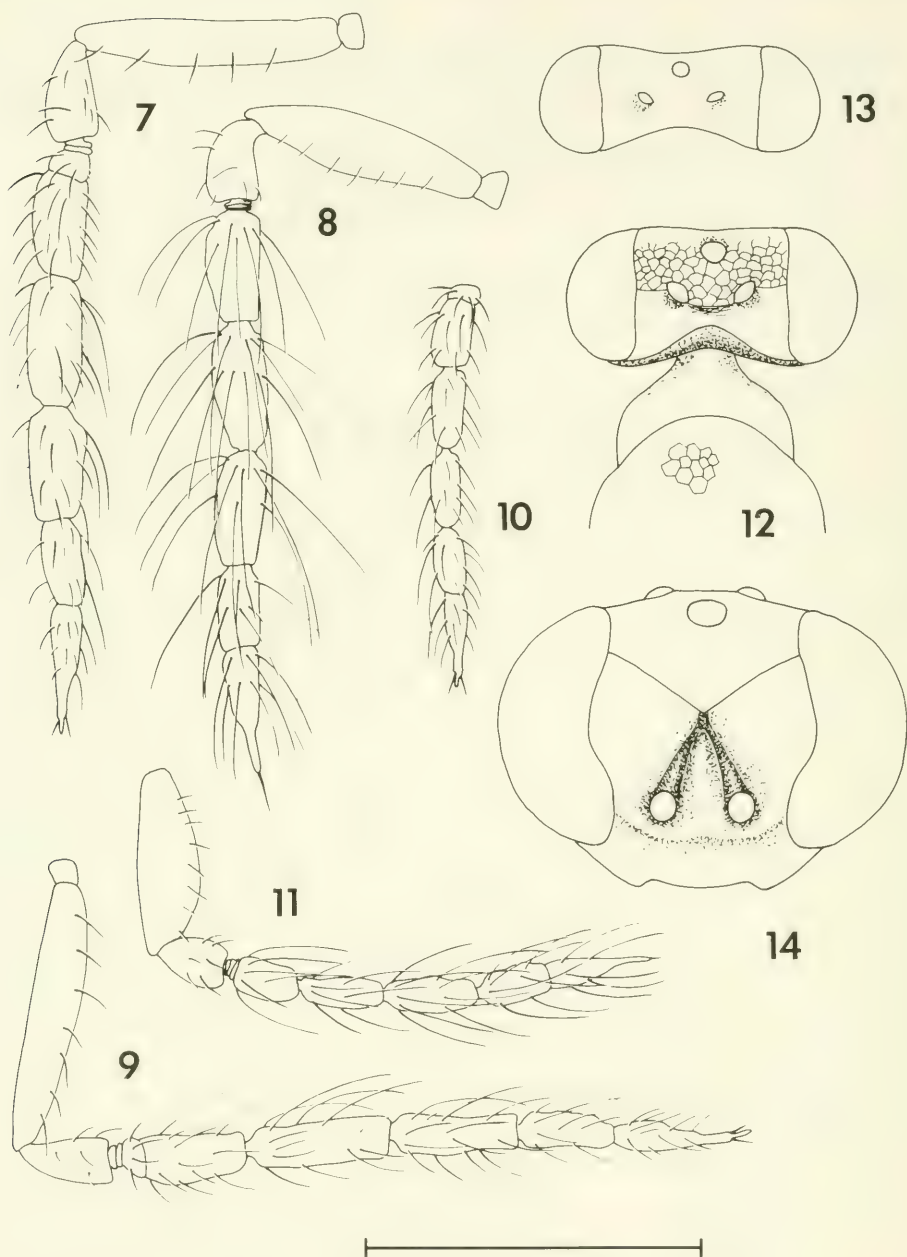
Male: Length of body: 1.0–1.3 mm. Head: Scape wider than in female. Frons below fork metallic bluish green. Flagellar segments I and IV about $2.0\times$, II and III $2.3\text{--}2.5\times$, and V about $3.5\times$ as long as wide. Ratios height of eye/malar space/mouth opening; $2.7/1.0/1.4$.

Thorax: Forecoxa dark and metallic, mid- and hindcoxae pale—predominantly dark and metallic.

Gaster: Ratio length of thorax + propodeum/length of gaster; $1.16\text{--}1.18$, $n = 3$.

Otherwise as in female.

Material studied.—Type material: Holotype *G. vonones* ♀ (BMNH Type No. 5.633); lectotypes *D. acutus* ♀ (BMNH Type No. 5.2409), *S. grenadensis* ♂ labelled



Figs. 7-13. *Zaommomyia* spp. 7, *Z. vonones* ♀, antenna. 8, same, ♂. 9, *Z. beckeri* ♀, antenna. 10, *Z. minuta* n. sp. ♀, flagellum. 11, same, ♂ antenna. 12, *Z. sulcata* ♀, head, pronotum and fore part of mesoscutum, dorsal view. 13, ditto ♂, head, dorsal view. Fig. 14, *Chrysocharis coptodiscae* Yoshimoto ♀, head, front view. Scale = 0.25 mm for the antennae, 0.50 mm for remaining illustrations.

"Chantilly Est. (Windward side) Grenada, W.I. H. H. Smith 14," "Cotype No. 6553 U.S.N.M.," "*Sympiesis grenadensis* How. ♂ type," lectotype hereby designated (USNM), (the type female of this species in BMNH is destroyed, with only legs remaining), *C. majoriani* ♂ labelled "Reared from leafminer of *Commelina*

virginica,” “St. Vincent B.W.I. 2.10.15,” “F. Watts Let. 2 May 16,” “20839” and paralectotypes 1 ♀ 1 ♂ (♀ head on slide) and one specimen with only thorax remaining, with same data as lectotype, lectotype and paralectotypes hereby designated. Additional material: USA: Florida 1 ♀, 1 ♀ ex *Liriomyza sorosis*, 1 ♀ ex *Agromyza parvicornis*, 1 ♂ labelled “Commelina” (all specimens in USNM); Texas 1 ♀ (CNC).

Hosts.—*Agromyza parvicornis* Loew and *Liriomyza sorosis* (Williston) (Diptera, Agromyzidae).

Distribution.—USA (Florida, Texas), Brazil and the West Indies.

***Zaommomyia beckeri* (Yoshimoto)**

Figs. 2, 3, 9

Chrysocharis beckeri Yoshimoto, 1973: 1386, NEW COMBINATION.

Diagnosis.—Horizontal arms of frontal fork V-shaped, thoracic dorsum usually with strong reticulation, mid- and hindcoxae pale, petiole pale, smooth, and globular.

Description.—*Female*: Length of body: 1.1–1.6 mm. Head: Scape completely pale or pale with apical part darkened, remainder of antenna dark and sometimes metallic. Flagellum with three apical segments more fused than basal two segments, segment I about $2.1\times$, II and III about $3.2\times$, IV about $2.7\times$, and V about $4.5\times$ as long as wide. Face and clypeus golden purple. Ratios height of eye/malar space/mouth opening; 6.8/1.0/3.1. Malar space as wide as width of scape. Frons below fork golden red or golden green, reticulation with low–quite high and fine–quite wide septa, with small meshes. Frontal fork Y-shaped. Lower triangle on frons above fork with color and reticulation as frons below fork, remaining parts on frons above fork metallic violet or bluish violet, reticulation very fine and engraved or smooth. Inner orbit of compound eye with one row of setae. Vertex inconspicuously metallic violet, reticulation like upper parts of frons above fork. Ratios POL/OOL/POO; 2.9/1.0/1.1. Occipital margin rounded. Ratio width of head/width of thorax across shoulders; 1.30.

Thorax (including propodeum): Pronotal collar without transverse carina. Mesoscutum and scutellum metallic greenish blue, bluish violet, golden green or a combination of these colors (scutellum sometimes completely or partly golden red), reticulation with high and wide septa (weaker in small specimens) with small meshes, notaular depressions with weaker reticulation. Dorsellum more or less flat, smooth and shiny or with very weak reticulation. Borderline between lower and upper epimeron curved. Forecoxa pale—predominantly dark, remaining parts of legs pale. Wings hyaline, forewing with or without a small fuscous spot below stigmal vein, rounded with speculum closed. Ratios length of marginal-/post-marginal-/stigmal veins; 8.8/2.1/1.0. Propodeum with same color as mesoscutum, the very anterior part of propodeum between spiracular sulci with a narrow groove, occasionally with complete carinae between petiolar foramen and spiracular sulci (as in *vonones*), with or without a complete median carina, and propodeal surface with quite weak—quite strong reticulation. Propodeal callus with 2 setae. Petiolar foramen rounded triangular.

Petiolus: Pale, smooth and globular.

Gaster: Oval, mean ratio length of thorax + propodeum/length of gaster; 0.78 ± 0.057 , $n = 10$.

Male: Unknown.

Material studied.—Type material: Holotype *C. beckeri* ♀ (CNC Type No. 12949). Additional material: CANADA: New Brunswick 1 ♀ (CNC); Ontario 12 ♀ (CH, CNC, LUZM); Quebec 5 ♀ (CH, LUZM). USA: Florida 5 ♀ (CH, CNC); Maryland 11 ♀ (CH, CNC); North Carolina 2 ♀ (CNC); Texas 5 ♀ (CH, CNC).

Distribution.—Canada (New Brunswick, Ontario, Quebec), USA (Florida, Maryland, North Carolina, Texas).

***Zaommomyia minuta*, NEW SPECIES**

Figs. 10, 11

Diagnosis.—Horizontal arms of frontal fork almost straight, all coxae pale, thoracic dorsum with fine and weak reticulation, petiole pale, smooth and globular in shape.

Description.—*Female*: Length of body: 0.8–1.1 mm. Head: Scape pale, remaining antenna dark. Two apical flagellar-segments fused, segment I about $1.7\times$, II and III about $2.5\times$, IV about $1.9\times$, and V about $3.9\times$ as long as wide. Face and clypeus golden purple. Ratios height of eye/malar space/mouth opening; $6.4/1.0/4.6$. Malar space as wide as width of scape. Frons below fork golden red, -purple, -green or purple, reticulation with low and narrow septa. Horizontal arms of frontal fork almost straight. Frons above fork metallic bluish violet or bluish-green, smooth and shiny. Inner orbit of compound eye with one row of setae. Vertex like frons above fork, color occasionally golden-green. Ratios POL/OOL/POO; $2.3/1.5/1.0$. Occipital margin rounded. Ratio width of head/width of thorax across shoulders; 1.22 .

Thorax (including propodeum): Pronotal collar without transverse carina. Mesoscutum metallic bluish violet or golden green, reticulation with very low and very narrow septa, and shiny. Scutellum golden red or, occasionally, with same color as mesoscutum, reticulation somewhat stronger than mesoscutum. Dorsellum convex, smooth and shiny. Borderline between lower and upper epimeron curved. Legs, including coxae, pale. Wings hyaline, fore wing rounded with speculum closed. Ratios length of marginal-/postmarginal-/stigmatal veins; $7.4/2.1/1.0$. Propodeum with same color as mesoscutum, entire surface smooth and shiny. Propodeal callus with 2 setae. Petiolar foramen rounded triangular.

Petiole: Pale, smooth and globular in shape.

Gaster: Oval, mean ratio length of thorax + propodeum/length of gaster; 0.92 ± 0.055 , $n = 10$.

Male: Length of body: 0.8–1.1 mm. Head: Scape wider than in female and pale brown. Flagellar segment I about $1.8\times$, II about $2.8\times$, III about $2.5\times$, IV about $2.0\times$, and V about $3.8\times$ as long as wide. Ratios height of eye/malar space/mouth opening; $5.8/1.0/3.4$.

Gaster: Mean ratio length of thorax + propodeum/length of gaster; 0.94 ± 0.081 , $n = 10$.

Otherwise as in female.

Types.—Holotype ♀ labelled; "TX: San Jacinto Co, 5 km S Cold-spring, 22.V.83, M. Kaulbars," "Holotypus *Zaommomyia minuta* Hansson." Paratypes: 6 ♀ 3 ♂ same locality as holotype; 9 ♀ 24 ♂ "TX: San Jacinto Co., 5 km S Coldspring, Double Lk Cpdg, 22–24.V.83, M. Kaulbars"; 11 ♀ 6 ♂ "TX: Bastrop Co., Bastrop St Pk, 24–27.V.83, M. Kaulbars"; 1 ♀ "FL: Liberty Co., Torreya St Pk, 7.X.1980, 8022 Masner & Bowen"; 1 ♂ "LA: Grant Parish, 28 km N Alexandria, Stuart Lk

Cpdg, 19.V-17. VIII.83, M. Kaulbars"; 1 ♀ "NC: Pamlico Co., Hwy 55 at Craven Co. junction, 15.X.1980, 8030 Masner & Bowen"; 1 ♀ "Can. B.C. Simon Fraser U., 26.IV.1979, Mal. Trap." Holotype and 33 paratypes in CNC, remaining paratypes in CH.

Distribution.—Canada (British Columbia) and USA (Florida, Louisiana, North Carolina, Texas).

Zaommomyia sulcata, NEW SPECIES

Figs. 5, 6, 12, 13

Diagnosis.—Male head in dorsal view short, vertex smooth and shiny behind lateral ocelli, malar space comparatively wide (about $2.5\times$ as wide as width of scape), pronotum elongate and campanuliform, thoracic dorsum flat, postmarginal vein only $1.6\times$ as long as stigmal vein, propodeum with two complete and parallel submedian grooves, petiole about $1.5\times$ as long as wide, dark and metallic with strong reticulation/sculpture and with anterodorsal part raised in a sharp edge covering petiolar foramen.

Description.—*Female*: Length of body: 1.3–1.5 mm. Head: Scape infusate, remainder of antenna dark. Flagellum with three apical segments more fused than basal two, segments I, II and III about $2.0\times$, IV about $1.7\times$, and V about $3.3\times$ as long as wide. Face and clypeus metallic purplish black. Ratios height of eye/malar space/mouth opening 2.9/1.0/1.4. Malar space $2.5\times$ as wide as width of scape. Frons below fork metallic purplish black, reticulation with quite high and narrow septa, meshes comparatively large. Frontal fork Y-shaped. Lower triangle on frons above fork flat with same color and reticulation as frons below fork, remaining parts of frons above fork metallic bluish-violet, occasionally purplish in parts and reticulation same as frons below fork. Inner orbit of compound eye with one row of setae. Vertex with part inside ocellar triangle and parts in front of lateral ocelli with same color and reticulation as upper parts of frons above the fork and parts behind lateral ocelli metallic violet and smooth. Ratios POL/OOL/POO; 1.7/1.1/1.0. Occipital margin with a blunt edge behind ocellar triangle, otherwise rounded. Ratio width of head/width of thorax across shoulders; 1.29.

Thorax (including propodeum): Pronotal collar without transverse carina, pronotum elongate and campanuliform. Thoracic dorsum flat. Mesoscutum metallic bluish violet, reticulation with quite high and quite narrow septa, meshes large. Scutellum golden red, reticulation same as mesoscutum, occasionally with smaller meshes. Dorsellum flat, smooth and shiny or with quite weak sculpture. Borderline between lower and upper epimeron curved. All coxae dark and metallic, fore- and midcoxae with weak and hindcoxa with strong reticulation. Remaining parts of legs pale. Wings hyaline, forewing rounded with speculum closed, costal cell very narrow. Ratios length of marginal-/postmarginal-/stigmal veins; 8.7/1.6/1.0. Propodeum with same color as mesoscutum, with two complete and parallel submedian grooves, surface otherwise smooth. Propodeal callus with 2 setae. Petiolar foramen small and rounded.

Petiolus: Dark and metallic, about $1.5\times$ as long as wide with strong reticulation/sculpture, with anterodorsal part raised in a sharp edge covering petiolar foramen (as in *Pediobius* Walker).

Gaster: Elongate-oval. Ratio length of thorax + propodeum/length of gaster; 0.76–1.00 $n = 4$.

Male: Length of body: 1.2 mm. Head: Scape slightly wider than in female and

completely dark. Head in dorsal view short. Flagellar-segment I about $2.3\times$, II about $2.5\times$, III about $2.6\times$, IV about $1.8\times$, and V about $3.8\times$ as long as wide. Ratios height of eye/malar space/mouth opening; $2.8/1.0/1.5$.

Gaster: Ratio length of thorax + propodeum/length of gaster; 0.91 , $n = 1$. Otherwise as in female.

Type material.—Holotype ♀ labelled; "FL: Jackson Co., Chattahoochee, 8024 Mosquito Ck, 8.X.1980, Masner & Bowen," "Holotypus *Zaommomyia sulcata* Hansson" (CNC). Paratypes: 3 ♀ 1 ♂ from same locality as holotype (1 ♀ in CH, remaining in CNC); 1 ♂ "Leeward side St. Vincent, W.I. H. H. Smith 201," "♂ Type No. 2472 USNM," "*Chrysocharodes petiolata* Ashm. ♂ Type" (USNM).

Distribution.—USA (Florida) and the West Indies (St. Vincent).

Remarks.—Compared to the other species in the genus, *sulcata* is an odd species. The pronotum, propodeum and petiole are quite different in *sulcata*, but because the antennae and frons are identical in all four species, I place them in the same genus. The male in the USNM is part of the syntype material of *Chrysocharodes petiolata* Ashmead. A lectotype, a headless female, has already been designated for this species by Bouček (1977: 8).

ACKNOWLEDGMENTS

I am grateful to L. Huggert (same address as author), J. S. Noyes (British Museum (Natural History)), M. E. Schauff (Systematic Entomology Laboratory, Agricultural Research Service, USDA) and C. M. Yoshimoto (Canadian National Collections) for loan of type and additional material. I thank also L. Huggert for reading the manuscript.

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**CARIBBEAN FRUIT FLIES, *ANASTREPHA SUSPENS*A (LOEW)
(DIPTERA: TEPHRITIDAE), REARED FROM EGGS
TO ADULTS ON CANNIBALISTIC DIET**

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Abstract. — In the laboratory Caribbean fruit flies, *Anastrepha suspensa* (Loew), were reared from eggs to adults on a cannibalistic diet. Starting 1 day after eclosion, larvae received as food only conspecific eggs or larvae newly eclosed from these eggs. Of one group of 20 larvae, 5 (4♂, 1♀) grew to adulthood. None in a second group of 20 larvae survived to adulthood. When fed water, sucrose and yeast hydrolysate enzymatic, the adults mated, and the female produced eggs from which at least one larva eclosed. Thus, *A. suspensa*, an herbivorous species, can develop into apparently normal adults in the absence of plant material.

Cannibalism is widespread in the animal kingdom, including a number of insect orders, and occurs normally in the field for a number of species (Fox, 1975). Herbivorous insects, as well as carnivores, engage in cannibalism (Kirkpatrick, 1957). Instances of cannibalism by herbivorous insects in the presence of abundant host plant material have been reported in nature and in the laboratory (Brower, 1961).

Although cannibalism may play a crucial role in the development, survival, and population dynamics of some insects, little is known about the development of herbivorous insects in the absence of plant material. The rearing of Caribbean fruit flies, *Anastrepha suspensa* (Loew), without fruit or artificial diet is reported here.

MATERIALS AND METHODS

The insects used in this study were from a laboratory colony maintained on the artificial larval diet described by Burditt et al. (1975). Flies laid eggs through the cotton sleeves of the screened aluminum rearing cages. The eggs were brushed off on successive days with a soft bristled paint brush, so that after the first day of a series of collections, the eggs removed were ≤ 24 h old. The eggs were rinsed in distilled water to remove nonviable eggs and debris, and soaked for 4 min in a 5% Clorox[®] (i.e. 0.05% sodium hypochlorite) solution to protect against contamination with ovicidal microorganisms. Again the eggs were rinsed with distilled water, and then soaked in a 0.03% sodium benzoate solution. After 4 min the eggs were poured onto a strip of Masslin[®] Sports Towel wrapped around an aluminum weighing boat (6 cm diam, 1.5 cm high), so that the portion of the strip covered with eggs was over the cavity of the boat. The eggs, thus arranged, were placed in a plastic tub (7.5 cm diam, 5 cm high), which was covered with a

transparent sheet of plastic affixed with a rubber band. Larvae eclosed 3 days after oviposition.

Four days after oviposition (i.e. 1 day after eclosion) 20 first instar larvae were placed, using forceps, on another strip of Masslin[™] towel wrapped around an aluminum weighing boat. The towel was moistened with 0.03% sodium benzoate solution. Ca. 20 mg of 1- or 2-day old eggs were piled on top of the larvae. The weighing boat with the towel and insects was placed inside a plastic tub, as previously described, and this was covered with a piece of transparent plastic held with a rubber band. All eggs and larvae were maintained at 22 to 25°C and a 16:8 photoperiodic regime. Additional batches of eggs (ca. 20 mg each), all 1 or 2 days old, were added every 1 or 2 days as long as the original larvae (noticeably larger than the younger ones eclosed from eggs provided as food) lived. After 9 days the 10 remaining original larvae were divided into two groups of five each, and set up in tubs and provided eggs as described. Larvae that occasionally crawled off the strip of towel were placed back under the pile of eggs. When the first larva attained the final instar, milled vermiculite was spread on the bottom of the weighing boats and tubs as a medium for pupariation.

Three or 4 days after formation, puparia were rinsed twice with distilled water and dried for 20 min on a paper towel. The puparia were held until adult emergence in a desiccator jar kept at 23 to 29°C in a 16:8 photoperiod. Water in the bottom of the desiccator jar maintained 100% RH within the jar. The puparia were kept until adult emergence.

Adults were held in a plastic tub (7.5 cm diam, 5 cm high) covered with plastic screen held in place with a rubber band. Water, sucrose and yeast hydrolysate were provided for nourishment. One week after at least one fly of each sex had emerged, a piece of parafilm (2 cm²) was appressed to the screen for egg deposition. One week later, a wad of moistened tissue paper was placed in a petri dish half (5 cm diam, 0.5 cm high) and the open end of the dish covered with a sheet of parafilm. This was placed in the cage (tub) for oviposition. Eggs laid through parafilm covering the petri dish were checked daily for eclosion. Adults and eggs were maintained at the same temperature and photoperiod as the puparia.

A second group of 20 1-day old larvae was divided into groups of 10 larvae each and maintained as was the first group.

As a comparison, two groups of 20 1-day old larvae were placed into plastic medicine cups (capacity ca. 25 ml) containing ca. 18 g artificial diet. Paper lids with a pin hole in them covered the cups. After 8 days milled vermiculite (ca. 8 ml) was added on top of the diet, and 2 weeks later the puparia removed. These control insects were otherwise subjected to the same maintenance procedures, temperature and relative humidities as those on the cannibalistic diet, except that adults were not held for oviposition.

Adults were dried for 24 h in ambient RH after having been stored with moist tissue in vials in freezer. Pronotal length and width of these specimens (all cannibals and 10 of each sex of controls) were measured.

RESULTS

Of the first group of 20 larvae, 5 (4♂, 1 ♀) developed into adults (Table 1). The rate of development of the cannibals was slower than that of larvae fed the artificial diet, and mortality was much higher. The surviving female, provided a standard

Table 1. Developmental times of *A. suspensa* reared on a diet of conspecific eggs and small larvae, and on an artificial diet.

	No. Formed Puparia	Range in Days Eggs to Puparia	No. Adults	Range in Days Puparia to Adults	Range in Days Eggs to Adults
Cannibals					
Group 1 ^a	8	16–23	5	13–16	29–39
Group 2	0		0		
Control	19	7–12	17	11–14	18–26

^a Started with 20 1-day-old larvae per group, and 20 controls.

adult diet of water, sucrose and yeast hydrolysate enzymatic, laid 24 eggs. However, she laid all but 6 of the eggs through the yeast hydrolysate smeared on the screen of the cage. Attempts to remove these eggs for maintenance under higher humidity were unsuccessful. One of the eggs laid through the parafilm covering the petri dish hatched. None of the second group of larvae formed puparia, although three attained the final instar.

Adults reared on the cannibalistic diet as larvae, although smaller, did not differ greatly in size from those reared on the artificial diet. Pronotal dimensions of the cannibals were 1.75 ± 0.24 mm long, 1.65 ± 0.19 mm wide for the males and 1.8 mm long, 1.8 mm wide for the female, while those for the flies reared on the artificial diet were 1.93 ± 0.08 mm long, 1.86 ± 0.05 mm wide for males ($n = 6$) and 1.9 ± 0.06 mm long, 1.8 ± 0.06 mm wide for females ($n = 6$). The weights of the cannibals were 4 ± 0 mg ♂, 5 mg ♀, and averaged 4.5 ± 0.84 mg ♂; 6.5 ± 1.87 ♀ for the controls.

DISCUSSION

The failure of any of the second group of larvae to develop as far as pupariation may have been due to a recurrence of an unidentified bacterial disease (T. Clark, pers. comm.), which had ravaged the stock colony several months earlier. Further evidence for disease was the scarcity of newly hatched larvae among the eggs provided as food during the last week larvae of the second group were alive.

Often larvae that crawled away from the eggs had to be replaced under the egg pile. This emigration indicates that although egg or larval cannibalism may be nutritionally adequate, the larvae did not adapt well to such a diet. Many of the larvae that died were found away from the egg mass. It is possible that as the original larvae grew and newly eclosed larvae began to feed, insufficient food was present.

It was not determined whether the larvae ate eggs or newly hatched larvae or both, or whether this food was dead or living when eaten. Microorganisms may have played an important nutritional role (Jones, 1983).

Cannibalism may be advantageous to organisms using rather ephemeral food sources such as fruit. *A. suspensa* larvae are ill equipped to search far for a second fruit should their initial fruit become depleted as a food source. Cannibalism would help to ensure that a fruit would not become overpopulated with larvae. Furthermore, cannibalism might provide the nutrition needed for larvae to complete development should their food supply become depleted or provide the nutrition needed for small larvae to move to more suitable parts of a fruit.

In an evolutionary context predacious or scavenging insects are thought by some to be ancestral to herbivores, and reversion to carnivory might take place more readily than for a carnivore to develop properly on a largely herbivorous diet (Southwood, 1973; Strong et al., 1984).

This study shows that *A. suspensa* can develop into apparently normal adults in the absence of fruit or plant derived food, and, thus, *A. suspensa* is not dependent on any chemical unique to plants for metamorphosis.

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TWO NEW FLIGHTLESS SPECIES OF *SCARITES* S. STR.
INHABITING FLORIDA AND THE WEST INDIES
(COLEOPTERA: CARABIDAE: SCARITINI)

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Abstract.—Two new flightless species of *Scarites* s. str., near *Scarites subterraneus* Fabricius, are described. *Scarites ocalensis* n. sp. is micropterous and is recorded from peninsular Florida north of Lake Okeechobee. *Scarites marinus* n. sp. is brachypterous and inhabits marine beaches of peninsular Florida, the Bahama Islands, Cuba, and the Yucatan Peninsula. A key and diagnoses are provided to aid in identification.

Incredible as it may seem, given the large number of described forms within the North American *Scarites subterraneus* complex, study of LeConte's type material at the Museum of Comparative Zoology (Harvard University) and Chaudoir's type material at the Muséum National d'Histoire Naturelle (Paris) has revealed two unrecognized species inhabiting Florida and the West Indies. Both species are flightless; *Scarites marinus* n. sp. is intertidal.

The *Scarites subterraneus* complex is defined here to include members of the genus *Scarites* possessing the following combination of characters: characteristics of *Scarites* s. str. (Bänninger, 1938: 114-116; Reichardt, 1977: 388); antennomeres 8-10 as broad as long (moniliform); anterior lateral seta of pronotum absent; metasternum asetose; in the New World restricted to North America. A neotype was designated for *Scarites subterraneus* Fabricius by Nichols (1985), thereby stabilizing the taxonomic identity of this species. This action also preserves the concept of the genus *Scarites* because *S. subterraneus* is the type species.

As defined above, the *Scarites subterraneus* complex excludes several other nearctic species of *Scarites* in the narrow sense. These species (including *Scarites quadriceps* Chaudoir, *Scarites substriatus* Haldeman, etc.) differ from members of the *Scarites subterraneus* complex in having antennomeres 8-10 distinctly longer than broad (filiform). Additional study is needed to work out the species limits among these species. A provisional key to the New World species of the *Scarites subterraneus* complex is provided after the descriptions of *S. ocalensis* n. sp. and *S. marinus* n. sp.

METHODS

Male and female genitalic characters have not been used to distinguish species of *Scarites* (see Bänninger, 1938). Based upon my own observations this is because the genitalia generally do not differ significantly among the species. The two species described here were delimited using consistently correlated, non-genitalic mor-

phological differences and apparent differences in ecology. Wing venation homologies and abbreviations in Figs. 6–8 were adapted from Wallace and Fox (1975).

Scarites marinus Nichols, NEW SPECIES

Figs. 1, 7, 9

Scarites californicus, Schwarz, 1878: 435; Blatchley, 1914: 62, 1917: 137; Darlington, 1936: 160 (nec LeConte). **MISIDENTIFICATION.**

Scarites subterraneus var. *californicus*, Schaeffer, 1913: 123 (in part); Leng, 1915: 567, 568 (nec LeConte). **MISIDENTIFICATION.**

Scarites sp. ?, Leng and Mutchler, 1914: 395; Bänninger, 1938: 139 (footnote); Darlington, 1953: 4.

Diagnosis.—Characteristics of *Scarites* s. str. (Bänninger, 1938: 114–116; Reichardt, 1977: 388); antennomeres 8–10 as broad as long (moniliform); postocular area not projecting laterally as far as compound eye, in dorsal view; anterior lateral seta of pronotum absent; metasternum asetose; metasternum behind mesocoxa longer than length of metacoxa; elytral striae very finely impressed, evanescent toward apex and possessing minute punctulae; setiferous puncture in basal half of interval 3 of elytron absent; brachypterous; small species, left elytron 5.85–9.05 mm in length; inhabiting marine beaches.

Description.—Characteristics of *Scarites* s. str. (Bänninger, 1938: 114–116; Reichardt, 1977: 388); habitus (Fig. 1); body black, antennae and palpi ferrugineous, legs piceous.

Head: Antennae with antennomeres 8–10 as broad as long (moniliform); compound eyes as in *S. subterraneus* (Fig. 4), postocular area not projecting laterally as far as compound eye (in dorsal view) and lacking a narrow ocular margin.

Thorax: Pronotum broadest about middle and lacking anterior lateral seta; metasternum asetose, behind mesocoxa slightly longer than metacoxa; metepisternum with anterior margin ca. $\frac{1}{2}$ length of lateral margin; elytral striae very finely impressed, evanescent toward apex and possessing minute punctulae; elytral intervals lacking microsculpture on disc, with isodiametric (hexagonal) microsculpture at sides and at extreme apex (at $75\times$); setiferous puncture in basal half of interval 3 almost always absent; brachypterous (Fig. 7); elytra together elongate oval, dorsal outline as in *S. subterraneus*.

Abdomen: No obvious differences in male or female genitalia from *S. subterraneus*.

Size: Length of left elytron: range (170 individuals), 5.85–9.05 mm (nearest .05); median, 8.15 mm (nearest .05); mean, 8.00 (nearest .05).

Measurements of female holotype: Maximum width of head before eyes, 3.28 mm (nearest .02 mm); maximum width of head, 3.80 mm (nearest .02); maximum width of pronotum, 4.55 mm (nearest .05); width of pronotum at hind angles, 4.05 mm (nearest .05); length of pronotum at midline, 3.20 mm (nearest .05); maximum width of elytra, 4.85 mm (nearest .05); length of left elytron, 8.15 mm (nearest .05).

Etymology.—Named for the habitat that this species occupies, namely marine beaches.

Type locality.—Big Pine Key, Florida (Monroe Co.).

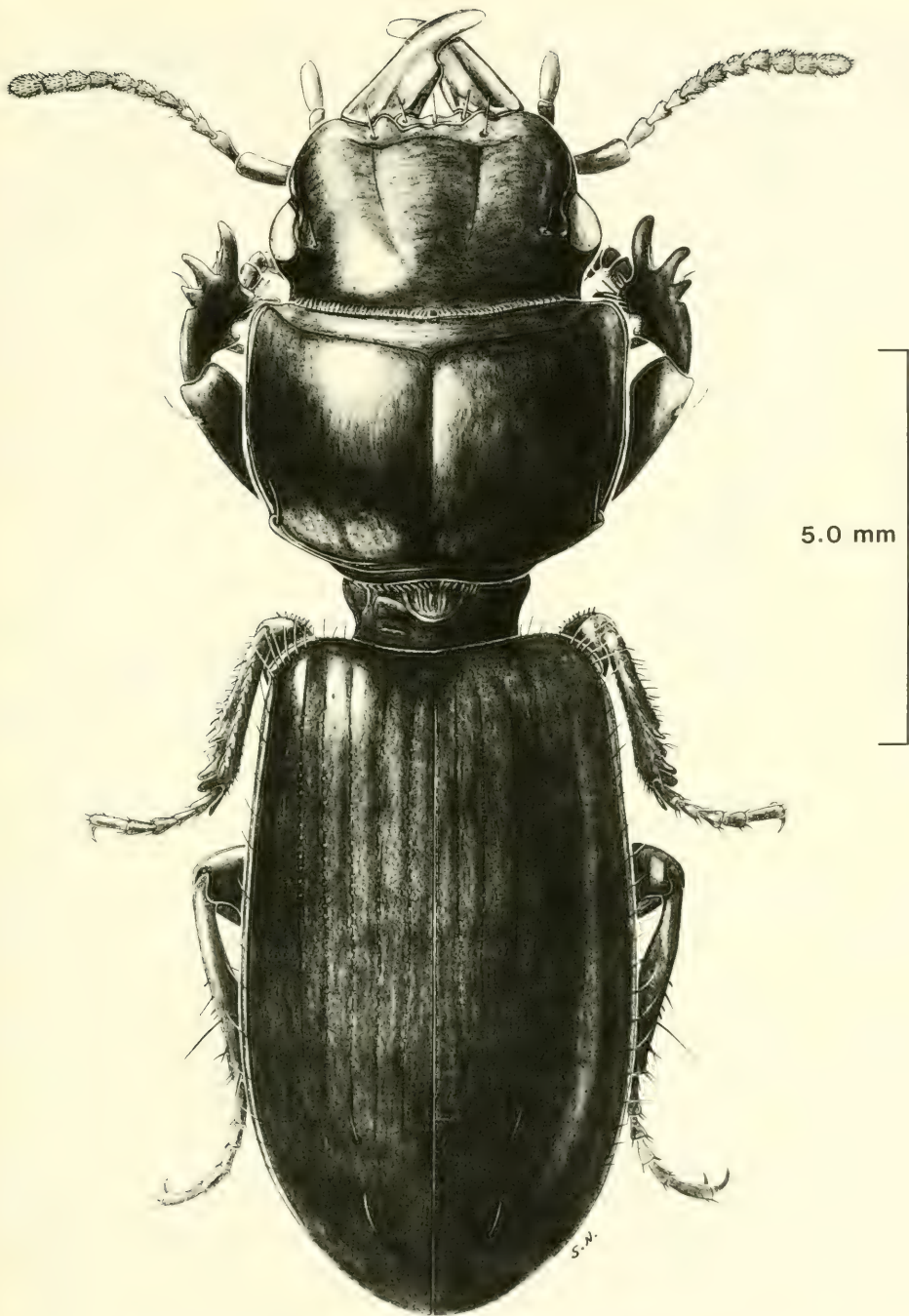
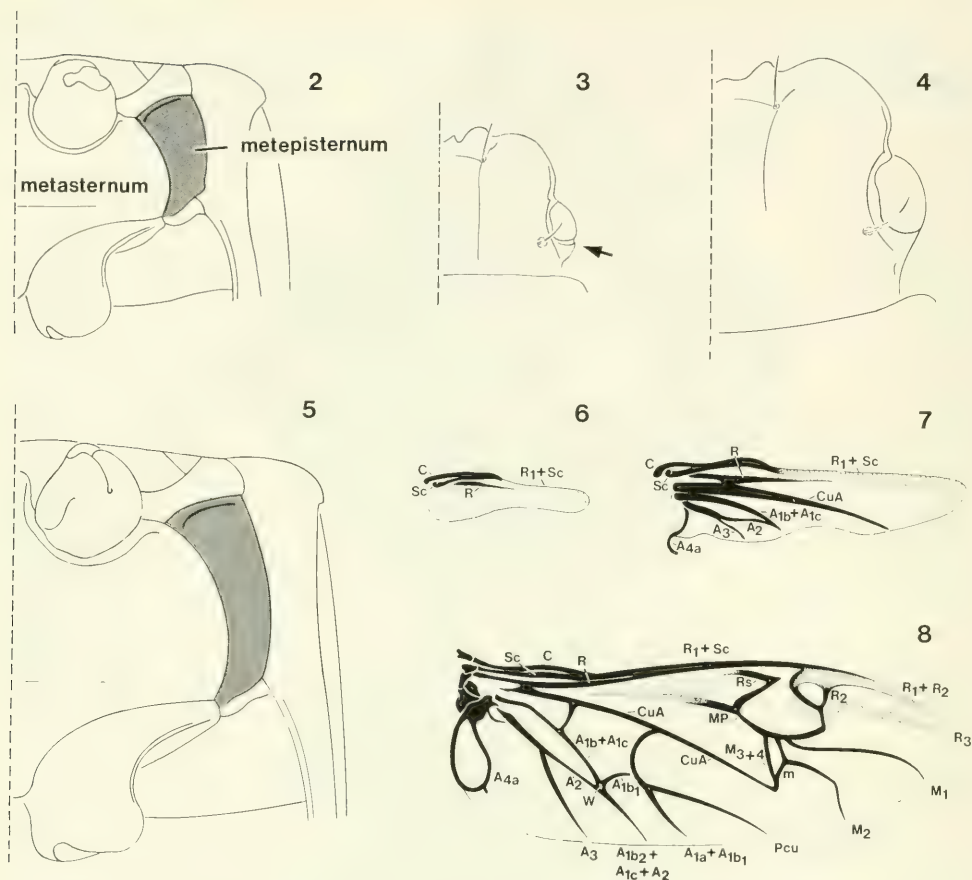


Fig. 1. Habitus, *Scarites marinus*. Mexico: Quintana Roo: Puerto Juarez.



Figs. 2–8. *Scarites* spp. 2, Pterothorax (oblique ventral view) of *S. ocalensis*. 3, Head (dorsal view) of *S. ocalensis*. 4, Head (dorsal view) of *S. subterraneus*. 5, Pterothorax (oblique ventral view) of *S. subterraneus*. 6, Metathoracic wing of *S. ocalensis*. 7, Metathoracic wing of *S. marinus*. 8, Metathoracic wing of *S. subterraneus*.

Distribution (Fig. 9).—Peninsular Florida, Bahama Islands, Cuba, and the Yucatan Peninsula. A single specimen without specific locality or date has been collected in Louisiana. See list of materials below for more exact locality information.

Ecology.—This species is apparently restricted to sea beaches, being commonly found beneath rotting seaweed. This species inhabits subtropical regions; the Cedar Keys (Levy Co., Florida) appear to have the northernmost established population. The species has been collected throughout the year. Teneral specimens were collected in January in the State of Campeche, Mexico.

Material examined.—*Holotype*: ♀, bearing the following labels: printed “FLA. Monroe Co. Big Pine Key, SE corner near US 1, 22 Dec. 1965 R. Beard”; handwritten, glued to red backing “HOLOTYPE *Scarites marinus* Nichols des. S. W. Nichols 1985.” Genitalia in glycerine-filled microvial affixed beneath final label. Holotype deposited in the Cornell University Insect Collections (CUIC). *Paratypes*

(169 individuals): FLORIDA: Dade Co.: Cutler (1, USNM), Matheson Hammock (2, CNCI). Levy Co.: Cedar Keys (3, MCZC, USNM), North Key (1, FDAG). Monroe Co.: Boca Chica nr. W. end SR 941 (1, FDAG), Cape Sable (31, FDAG, PUIC), Big Pine Key (2, FDAG, OSUC), Flamingo (1, JHFC), Key Largo (2, FDAG), Key West (1, USNM), Long Pine Key (1, MCZC), Lower Matecumbe Key (2, FDAG, MCZC), No Name Key, 7 mi. E. bridge (1, FDAG). Pinellas Co.: Dunedin (6, AMNH, PUIC, USNM), Maximo Point (3, PUIC), St. Petersburg (3, CUIC, MCZC-H. C. Fall Collection). Sarasote Co.: Sarasota (1, MCZC). BAHAMA ISLANDS: Eleuthera (1, USNM). CUBA: La Habana Prov.: Havana (1, MCZC). Pinar del Rio Prov.: Cayo Inez de Sota (1, ZMUA). YUCATÁN PENINSULA (MEXICO): Campeche: Campeche (1, MCZC), nr. Cuba (33, UASM), Zacatal (1, UASM). Quintana Roo: Cozumel Is., North Point (20, USNM), Isla Mujeres (5, USNM), Espiritu Santo Bay (1, USNM), Puerto Juarez (26, UASM). Yucatán: the state? (2, CNCI, USNM), Progreso (1, USNM). LOUISIANA: no specific locality (1, MCZC).

Scarites ocalensis Nichols, NEW SPECIES

Figs. 2, 3, 6, 10

Diagnosis.—Characteristics of *Scarites* s. str. (Bänninger, 1938: 114–116; Reichardt, 1977: 388); antennomeres 8–10 as broad as long (moniliform); postocular area projecting laterally as far as compound eye, in dorsal view; anterior lateral seta of prothorax absent; metasternum asetose; metasternum behind mesocoxa as long as or slightly shorter than length of metacoxa; elytral striae well-impressed to apex and lacking punctulae; setiferous puncture in basal half of interval 3 of elytron present or absent; micropterous; small species, left elytron 6.05–7.40 mm in length; known only from peninsular Florida.

Description.—Characteristics of *Scarites* s. str. (Bänninger, 1938: 114–116; Reichardt, 1977: 388); body black, antennae and palpi ferruginous, legs piceous.

Head: Antennae with antennomeres 8–10 as broad as long (moniliform); eyes somewhat reduced (Fig. 3), postocular area projecting laterally as far as compound eye (in dorsal view) and possessing a narrow ocular margin.

Thorax: Pronotum broadest before middle and lacking anterior lateral seta; metasternum asetose, behind mesocoxa as long or slightly shorter than metacoxa; metepisternum with anterior margin $\frac{1}{2}$ or more the length of lateral margin (Fig. 2); elytral striae well-impressed to apex and lacking punctulae; elytral intervals with distinct isodiametric (hexagonal) microsculpture throughout (at $75\times$); setiferous puncture in basal half of interval 3 of elytron present or absent; micropterous (Fig. 6); elytra together ovate, sides of elytra distinctly less parallel than in *S. subterraneus*.

Abdomen: No obvious differences in male or female genitalia from *S. subterraneus*.

Size: Length of left elytron: range (13 individuals), 6.05–7.40 mm (nearest .05); median, 6.80 mm (nearest .05); mean, 6.80 mm (nearest .05).

Measurements of male holotype: Maximum width of head before eyes, 3.32 mm (nearest .02); maximum width of head, 3.80 mm (nearest .02); maximum width of pronotum, 4.35 mm (nearest .05); width of pronotum at hind angles, 3.80 mm (nearest .05); length of pronotum at midline, 3.35 mm (nearest .05);

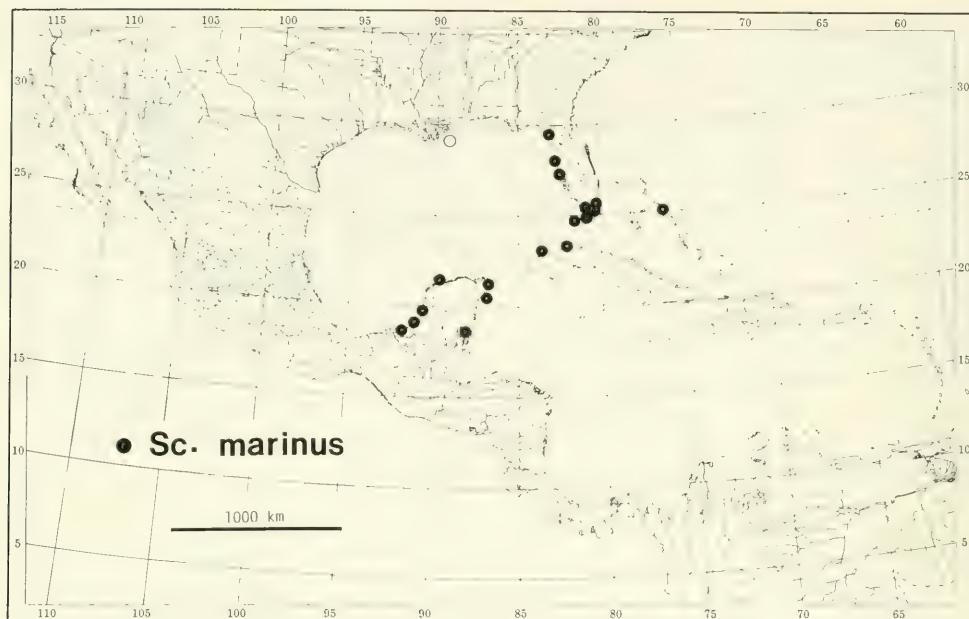


Fig. 9. Known distribution of *S. marinus* (open circle, state record for Louisiana).

maximum width of elytra, 4.25 mm (nearest .05); length of left elytron, 7.20 mm (nearest .05).

Etymology.—Named after the Ocala Island (i.e. highlands of peninsular Florida), a piece of land periodically isolated by eustatic fluctuations in sea level during the Pleistocene and probable area of origin of the species.

Type locality.—Jacksonville, Florida (Duval Co.).

Distribution (Fig. 10).—Known only from northern peninsular Florida north of Lake Okeechobee. See list of materials below for more exact locality information.

Ecology.—Collected between March 17 and June with no teneral specimens recorded. Nothing is known about this species' habitat. Judging from its flightless condition and reduced eyes *S. ocalensis* is probably not riparian, but instead probably lives in earthen tunnels in upland areas. This species inhabits the moist subtropical ("citrus growing") zone of Florida in the Holdridge system of life zones (Sawyer and Lindsey, 1964).

Material examined.—*Holotype*: ♂, bearing the following labels: handwritten "Jacksonville 3.May.16 Fla."; handwritten "Scarites subterraneus F. det. H. Dietrich"; male sex label; handwritten, glued to red backing "HOLOTYPE Scarites ocalensis Nichols des. S. W. Nichols 1985." Genitalia in glycerine-filled microvial affixed beneath final label. Holotype in Cornell University Insect Collections (CUIC). *Paratypes* (12 individuals), all from Florida. Alachua Co.: Gainesville (1, USNM). Duval Co.: Jacksonville (1, MCZC). Highlands Co.: Brighton (1, MCZC). Hillsborough Co.: no specific locality (1, USNM). Orange Co.: Winter Park (2, MCZC). Pinellas Co.: Gulfport (1, MCZC-H.C. Fall Collection). Seminole Co.: Sanford (3, MCZC). Volusia Co.: Enterprise (2, OSUC).

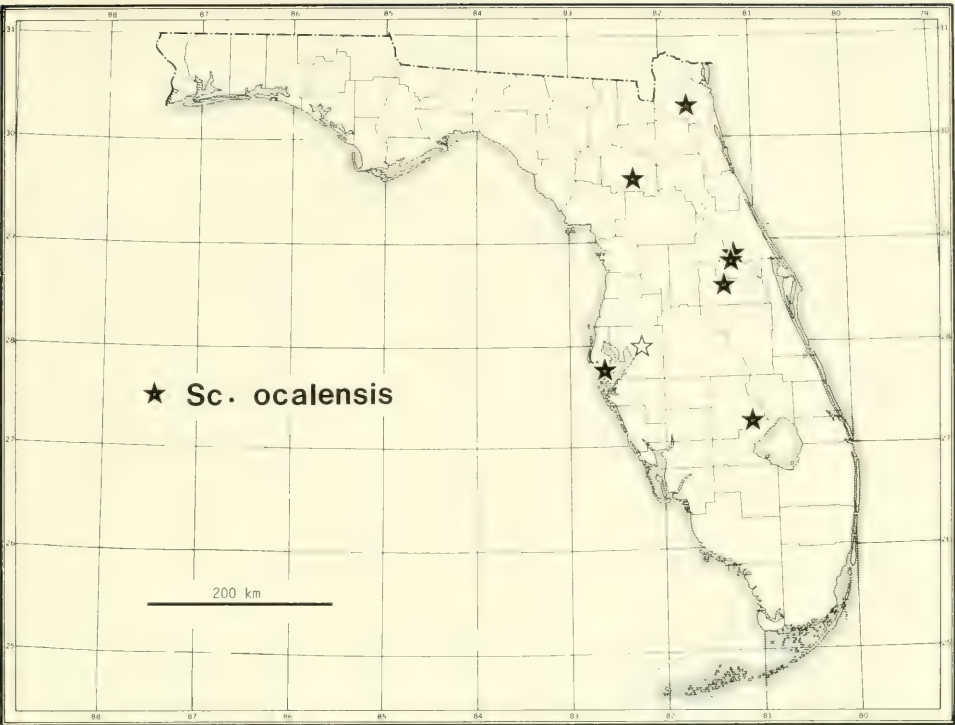


Fig. 10. Known distribution of *S. ocalensis* (open star, county record for Hillsborough Co.).

PROVISIONAL KEY TO THE NEW WORLD SPECIES OF THE
SCARITES SUBTERRANEUS COMPLEX

- 1. Metasternum and metepisternum reduced in length (Fig. 2); micropterous (Fig. 6); compound eye somewhat reduced, leaving narrow postocular border (Fig. 3); small species, left elytron not over 7.5 mm in length; Florida *ocalensis* n. sp.
- Metasternum and metepisternum not reduced in length (Fig. 5); brachypterous or fully winged (Figs. 7, 8); compound eye not reduced (Fig. 4); small to moderate sized species, hindbody generally over 7.5 mm in length; Florida and elsewhere 2
- 2. Setiferous puncture in basal half of elytral interval 3 absent (Fig. 1); elytral striae consisting of very finely impressed lines with minute punctulae; brachypterous (Fig. 7); distributed on sea beaches of the Gulf coast and the West Indies *marinus* n. sp.
- Setiferous puncture in basal half of elytral interval 3 usually present; elytral striae varying from virtually absent (some western *Sc. subterraneus*) to consisting of well-impressed grooves, but always lacking minute punctulae; fully winged (Fig. 8); not generally found on sea beaches 3
- 3. Larger species, left elytron over 10.0 mm in length; 7th elytral interval somewhat raised just behind humerus; median pair of setiferous punctures on abdominal sternum VII (last visible abdominal sternum) shifted away from posterior margin; Cuba *alterans* Chaudoir

- Smaller species, left elytron usually under 10.0 mm in length; 7th elytral interval not raised behind humerus; median pair of setiferous punctures on abdominal sternum VII not shifted away from posterior margin; Cuba and elsewhere *subterraneus* Fabricius

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A SPECIES OF FLEA (SIPHONAPTERA) ASSOCIATED WITH PORCUPINES COLLECTED IN SOUTH DAKOTA

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Abstract. — The flea *Chaetopsylla setosa* Rothschild is recorded for the first time from porcupines. This also extends the geographic range of *C. setosa* to include South Dakota. Geographic and host records are given for *C. setosa*.

Most mammals with spiny fur or quills lack characteristic fleas. Where such ectoparasites do occur, they are highly modified structurally, as in the case of *Parodontis riggenbachi* (Rothschild), a flea of porcupines in Asia and Africa (Traub, 1980). There have been few reports of fleas on the nearctic porcupine, *Erethizon dorsatum* L. The earliest record was that of a single female collected in northwestern British Columbia described by Jordan (1932) as *Ceratophyllus adustus*. Smit (1983) placed the species in the new genus *Celeophilus*. Haas et al. (1980) suggested that *C. adustus* is a nest flea of woodpeckers, and Jordan's unique specimen came from a porcupine that had climbed a tree with a woodpecker's tree hole nest. Smit (cited as in litt. by Traub et al. (1983)), believed that *C. adustus* had also been collected from owls in the U.S., but this has not yet been confirmed. Dunn and Parker (1923) reported *Orchopeas howardi* (Baker) (cited as *Ceratophyllus wickhami* (Baker) from porcupines in the Bitter Root Valley of Montana, but Jellison and Senger (1973) stated that the fleas were actually *Orchopeas caedens* (Jordan), a common parasite of tree squirrels of the genera *Sciurus* and *Tamiasciurus*. The only other siphonapteran to be reported from North American porcupines is *Epitedia wenmanni* (Rothschild), collected in Massachusetts (Main, 1970). The present report adds a fourth species, namely *Chaetopsylla setosa* Rothschild 1906, to the list of fleas on these porcupines.

Two collections of these fleas were taken from porcupines in the northwestern part of Harding County, South Dakota. One lot contained 18 females and 6 males, and 7 females and a single male were taken from a second host. Abdomens of all females were swollen with eggs. *Chaetopsylla setosa* is well known as a parasite of bears and other carnivores in British Columbia and Montana. The only other ectoparasite collected in this study was *Eutrichophilus setosus* (Giebel), a common chewing louse of *Erethizon dorsatum* throughout the United States.

Collection data of the two porcupines includes the following: specimen number 20 (J156), male, 15 Dec. 1976, '733-200-93 = 8050 gm, captured 1.5 mi W of Hy. 79 on Hy. 20, Harding County, South Dakota; specimen no. 22 (J158), male, 22 Dec. 1976, 648-198-86-18 = 5750 gm, captured 0.6 mi S of Custer National Forest Northern boundary on Hy. 79.

The only known carnivores in this part of South Dakota that could serve as sources of *C. setosa* include coyotes, red fox, and bobcats. Bears have not been reported to occur in this area of South Dakota since 1910 (Andersen and Jones, 1971). Coyotes have been collected in Harding County by Schitoskey (pers. comm.), but to date no infestations of *C. setosa* have been found. However, Easton (1982) reported *Pulex irritans* L. from coyotes from Harding County. He also collected *Vulpes velox* Merriam, another potential carnivore host, in Shannon County. The occurrence of fleas on porcupines is a new host record, and extends the eastern distribution of *C. setosa* to northwestern South Dakota.

Geographic and host records for *C. setosa* include *Canis latrans* Say and *Ursus americanus* Pallas in the original description of the female by Rothschild (1906). Other records include *Ursus horribilis* Ord by Spencer (1936) and Wagner (1936); *Lynx canadensis* Kerr, *Ursus* sp., *Gulo luscus* (L.) by Holland (1949, 1985); *Canis latrans*, *Ursus americanus*, *Gulo gulo luscus* (L.), by Hopkins and Rothschild (1956), all from British Columbia, Canada. In the United States *C. setosa* has been collected in Montana from *Canis latrans* in Carter, Lake and Petroleum counties; from *Felis concolor* Goldman in Mineral County, west of Missoula, and from *Ursus americanus* in Lincoln County (Jellison et al., 1943; Hubbard, 1947). Senger (1966) listed *Lynx rufus*, in Missoula County, east of Missoula, *Ursus americanus* and *U. horribilis*, in Flathead County east of Kalispell, and a "human" in Ravalli County. Jellison and Senger (1937), included records cited in earlier reports. There is an unpublished record that has included mink as a host of *C. setosa*.

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STUDIES IN NEOTROPICAL LEPTOCERIDAE (TRICHOPTERA), VI:
IMMATURE STAGES OF *HUDSONEMA FLAMINII* (NAVÁS) AND
THE EVOLUTION AND HISTORICAL BIOGEOGRAPHY OF
HUDSONEMINI (TRIPLECTIDINAE)

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Abstract. — The larval and pupal stages of the Chilean species *Hudsonema flaminii* (Navás) (Triplectidinae: Hudsonemini) are described and illustrated for the first time. The larva is characterized by the presence of secondary setae on the lateral sclerite of each anal proleg and by the brown-spotted head and thorax. Adult genitalia and wing venation of both sexes are redescribed and illustrated. A key to adults of the Neotropical triplectidine genera is provided. *Triplectides fazi* Navás is a synonym of *H. flaminii*, **New Synonym**. The evolution and historical biogeography of the Hudsonemini are discussed. *Hudsonema* is most closely related to the Australian genus *Condoceris*; its distribution conforms to a New Zealand-South American trans-Antarctic biogeographical track.

The long-horned caddisfly genus *Hudsonema* Mosely contains three described species: *H. aliena* (Mac Lachlan), *H. amabilis* (Mac Lachlan), both from New Zealand, and *H. flaminii* (Navás), an austral South American endemic. The distributions of these species conform to a trans-Antarctic, Australasian-Neotropical biogeographical track. Within the Trichoptera, exclusively trans-Antarctic distributions are found in the families Helicophidae, Kokiriidae, Philorheithridae, and Tasimiidae, and, within the Leptoceridae, in the genera *Hudsonema*, *Notalina*, and *Triplectides* (Holzenthal, 1986). *Hudsonema*, however, is the only leptocerid genus that exhibits an exclusively New Zealand-South American trans-Antarctic track, considered by Craw (1979, 1982) to be distinct from the Australian-South American trans-Antarctic track displayed by *Notalina* and *Triplectides*.

Mosely (1936) erected the genus *Hudsonema*, designated the New Zealand species *Tetracentron amabile* Mac Lachlan as the type species and transferred two South American species, *Triplectides discolor* Navás and *Triplectides flaminii* Navás, to his new genus. Later, Mosely and Kimmins (1953) transferred an additional New Zealand species, *Leptocerus alienus* Mac Lachlan to *Hudsonema* and described two new species, *H. maculata* and *H. sparsa*, both from Australia and Tasmania. Neboiss (1977) recognized that the two Australian species, *H. maculata* and *H. sparsa*, differed considerably from the type species in both genitalic and venational characters and transferred them to a new genus, *Noto-perata* Neboiss. Flint (1974) synonymized *H. discolor* (Navás) with *H. flaminii* (Navás). A specimen from the NMNH bearing the labels "CHILE: Valpo. Est.

Marga-Marga, nr. Perales 9 Mar. 1968 Flint & Pena" and "COMP. w. TYPE *Triplectides fazi* Nav. by Flint '76" is in fact a female of *Hudsonema flaminii*. I accept Flint's determination and consider *Triplectides fazi* Navás, 1932, to be a junior synonym of *Hudsonema flaminii* (Navás), 1926, **New Synonym**. The adult male and female genitalia and wing venation of *Hudsonema flaminii* have been described and illustrated previously by Mosely (1936, fig. 63–66) and Schmid (1950, fig. 105–110). Cowley (1978) described the larvae of the two New Zealand species and briefly discussed their biology. In the present paper, the larval and pupal stages of *Hudsonema flaminii* are described and figured for the first time. Redescriptions and illustrations of the adults of both sexes are also provided. A key to adults of the Neotropical triplectidine genera is included. Finally, the evolution and historical biogeography of the Hudsonemini are discussed.

Terminology for wing venation and female genitalia follows the review by Schmid (1980) and that for male genitalia, those of Nielsen (1957), Morse (1975), and Schmid (1980). Terminology for larval and pupal morphology follows the reviews by Wiggins (1977, 1984). Larval setal nomenclature and homology follows that of Williams and Wiggins (1981). All material examined is from the collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH). Distribution data are indicated by country and province. Complete collection records for only those specimens examined in preparing larval and pupal descriptions and illustrations are provided below.

***Hudsonema flaminii* (Navás)**

Figs. 1–5

Triplectides flaminii Navás 1926: 335, fig. 49 a–b; Navás 1929: 24; Navás 1930: 363.

Triplectides discolor Navás 1932a: 83, fig. 13; Navás 1933: 234.

Hudsonema flaminii, Mosely 1936: 111, fig. 63–68; Schmid 1950: 361, fig. 105–108; Flint 1967: 60; Flint 1974: 90, distribution.

Hudsonema discolor, Mosely 1936: 114; Schmid 1950: 362, fig. 109–110; Flint 1974: 84, synonym of *H. flaminii*.

Triplectides fazi Navás 1932b: 84, fig. 73; Mosely 1936: 126. **New Synonym**.

Adult: Tibial spur formula 2, 2, 4. Forewing (Fig. 5A) with forks I and V present in male; I, III, and V present in female; fork I distinctly petiolate; discal and thyridial cells subequal in length. Hindwing (Fig. 5B) with forks I, III, and V present in both sexes; forks I and V deep; discal cell present. General body color brown, with scattered white hairs on head and thorax; longitudinal white bands of hairs on forewing, especially in male (Mosely 1936, fig. 63); female forewing sometimes completely brown. Length of forewing 13–15 mm male, 9–11 mm female.

Male: Abdominal segment IX annular, anterior margin sinuate; tergum IX produced posteriorly, rounded in dorsal view, and forming dorsal shelf over bases of preanal appendages; lateral portions of IX produced posteriorly as setose, finger-like to triangular projections (Figs. 3A, 3B). Segment X with pair of long, slender, dorsomesal processes and pair of long, thin, gradually upturned, ventrolateral processes; ventrolateral processes each terminating in single seta (Figs. 3A, 3B). Preanal appendages broad, flat, heavily setose; apices acute (Fig. 3B). Inferior

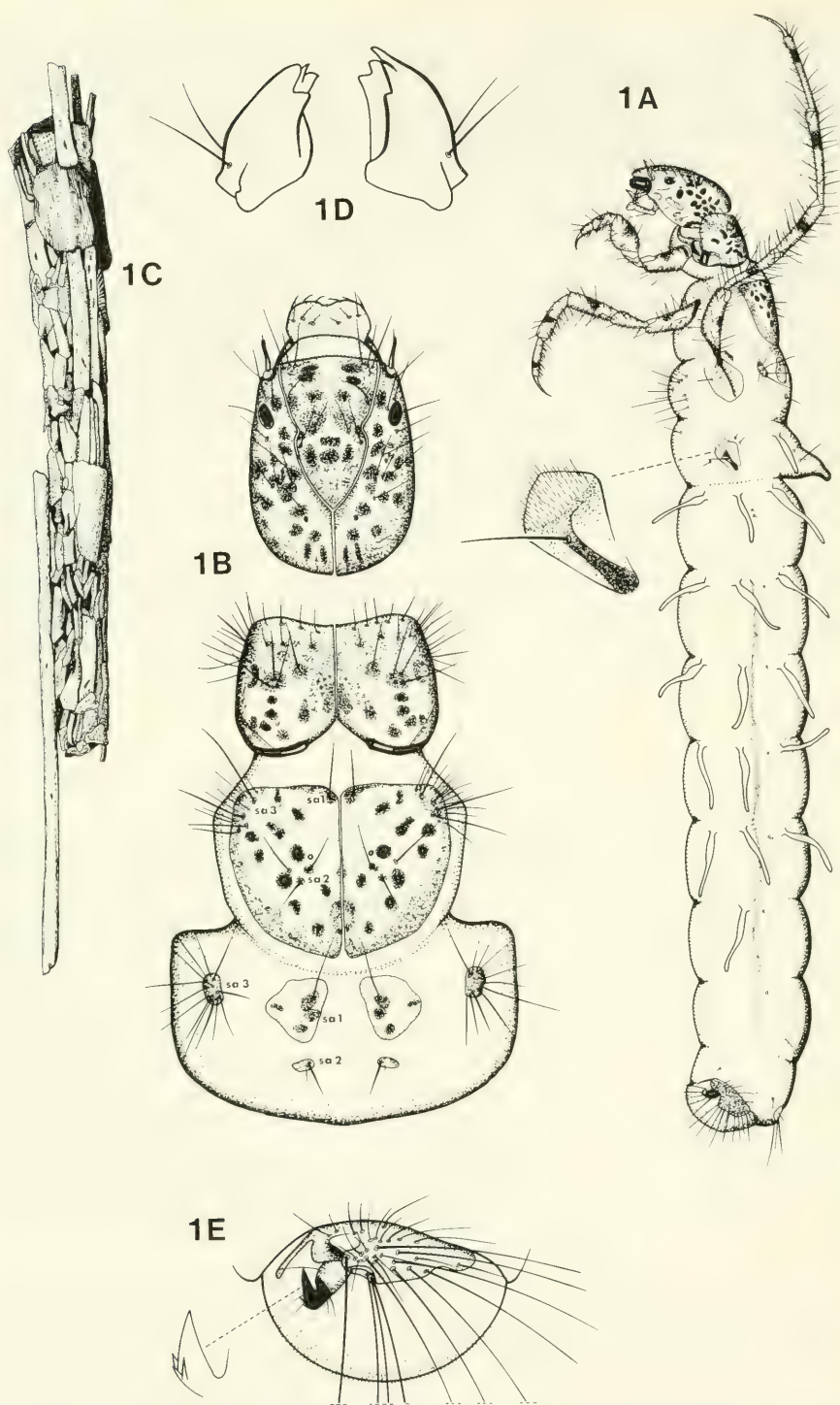


Fig. 1. *Hudsonema flaminii* (Navás), larva and case. A, Larva, lateral, lateral hump sclerite enlarged. B, Head and thorax, dorsal. C, Case, lateral. D, Mandibles, ventral. E, Anal proleg and abdominal segment X, lateral, anal claw enlarged.

appendages short and stout, more or less quadrate in general outline in lateral view (Fig. 3A); each with 4 terminal processes: dorsolateral (*dl*) and ventrolateral (*vl*) processes short, thumb-shaped in ventral view (Fig. 3C); ventromesal process (*vm*) short, slender, inconspicuous; dorsomesal process (*dm*) long, somewhat sinuate, sharply pointed; ventrobasal angle broadly rounded in lateral view, subrectilinear and next to the meson in ventral view; inferior appendages broadly connected basally (Fig. 3C). Phallic apparatus simple, short and slender; phallotremal sclerite with dorsal projections (Fig. 3D).

Female: Sternum IX distinctive; developed into broad, slightly concave, sclerotized plate; posterior portion shaped somewhat like head of a planarian (Fig. 4B). Valves long, flat, each bordered ventrally with short setae; appendages of segment X short, heavily setose (Figs. 4A, 4B).

Egg: Unknown.

Larva: Head (Figs. 1A, 1B, 2A): oval; ventral apotome long, rectangular, completely separating genae ventrally; subocular ecdysial line absent; head setal pattern as in Fig. 2A, typical for family; mandibles short and wide, with short rounded teeth surrounding central concavity (Fig. 1D). Thorax (Figs. 1A, 1B): pronotum lacking anterolateral ecdysial lines, anterolateral corners with many setae; mesonotum covered by pair of large sclerites; each with single seta at *sa1* position, 3 setae at *sa2* position, and many setae at *sa3* position; metanotum with large *sa1* sclerites, each bearing single, long, anteromesal seta; small *sa2* sclerites, each bearing 2 setae, one long, one very short; *sa3* sclerites each bearing about 13 long setae; metasternum with broad, transverse patch of approximately 70 setae. Head and thoracic sclerites yellowish-brown, with many dark brown maculations as indicated in Fig. 1B. Legs long, slender, each bearing numerous long setae; yellowish brown in color; each leg segment with darkly pigmented, subterminal band (Fig. 1A). Abdomen (Fig. 1A): lateral hump sclerite of abdominal segment I as in Fig. 1A insert; lateral fringe present on segments III–VII; lateral tubercles present on segment VIII; segments I–VIII each with 1 or 2 pairs of very short, lateral setae; abdominal gills single, distributed as in Fig. 1A; dorsal sclerite of segment IX with 3 pairs of setae: long lateral and mesal pair and very short pair situated between those pairs; lateral sclerite of anal proleg large, bearing about 20 secondary setae; anal claw with 3 small dorsal accessory hooks; wide band of minute spines bordering anal opening (Fig. 1E). Length of larva 10–13 mm.

Larval case: Composed largely of plant fragments, rough, very slightly curved and tapered; often with 1 or more twigs extending beyond posterior end (Fig. 1C). Length of case 20–30 mm (excluding trailing twigs).

Pupa: Head (Fig. 2C): 2 pairs of long frontal setae; 1 pair of setae on vertex; 2 setae on each antennal scape; 2 setae below each eye; labrum with 6 pairs of long setae; mandibles long and slender, with fine serrations along inner margins; 2 setae on the lateral base of each mandible. Abdomen: gills, setation, and hook plates as in Fig. 2B; segment IX with small, dorsolateral protuberances, each bearing about 5 long setae; anal processes each long and slender, apical portion curved outward and bearing 4 setae (Fig. 4B). Long trailing twigs of larval case generally trimmed off before pupation. Rock fragments incorporated into anteroventral end of pupal case; anterior and posterior ends closed off with silk and debris.

Distribution. — Argentina: Chubut, Neuquén, Río Negro. Chile: Aconcagua, Ar-

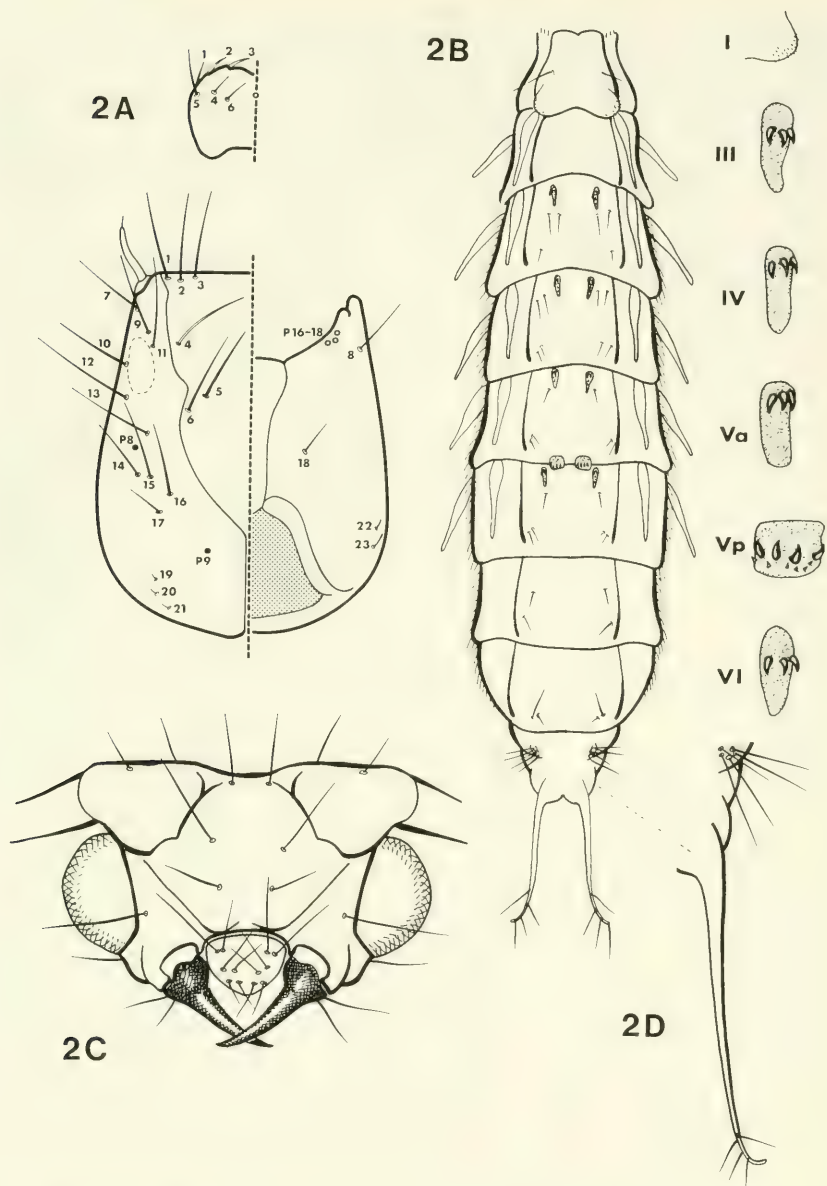


Fig. 2. *Hudsonema flaminii* (Navás), larva and pupa. A, Larva, head and labrum (detached) setal pattern, left half dorsal, right half ventral. B, Pupa, abdomen, dorsal, hook plates enlarged. C, Pupa, head, frontal. D, Pupa, right anal process, dorsal.

auco, Atacama, Bío-Bío, Cautín, Chiloé, Concepción, Coquimbo, Curicó, Linares, Malleco, Maule, Ñuble, O'Higgins, Osorno, Santiago, Valdivia, Valparaíso.

Material examined.—Argentina: Chubut: Arroyo Golondrinas, 6 km N Lago Puelo, 8.ii.1974, O. S. Flint, Jr., many larvae; Lago Puelo, 8.ii.1974, O. S. Flint, Jr., many larvae; Río Epuyen, Hoyo de Epuyen, 10.ii.1974, O. S. Flint, Jr., one larva. Neuquén: 2 km SE Lago Lolog, 22.i.1974, O. S. Flint, Jr., many larvae; 5

km SE Lago Huechulafquen, 26.i.1974, O. S. Flint, Jr., many larvae, prepupae. Río Negro: 5 km S Río Villegas, 7.ii.1974, O. S. Flint, Jr., female pupa, prepupae; Cascada Mallin Ahogado, El Bolson, 9.ii.1974, O. S. Flint, Jr., many male, female pupae. Chile: Malleco: Río Dumo, 11 km N Victoria, 300 m, 25.i.1978, C. M. & O. S. Flint, Jr., many larvae.

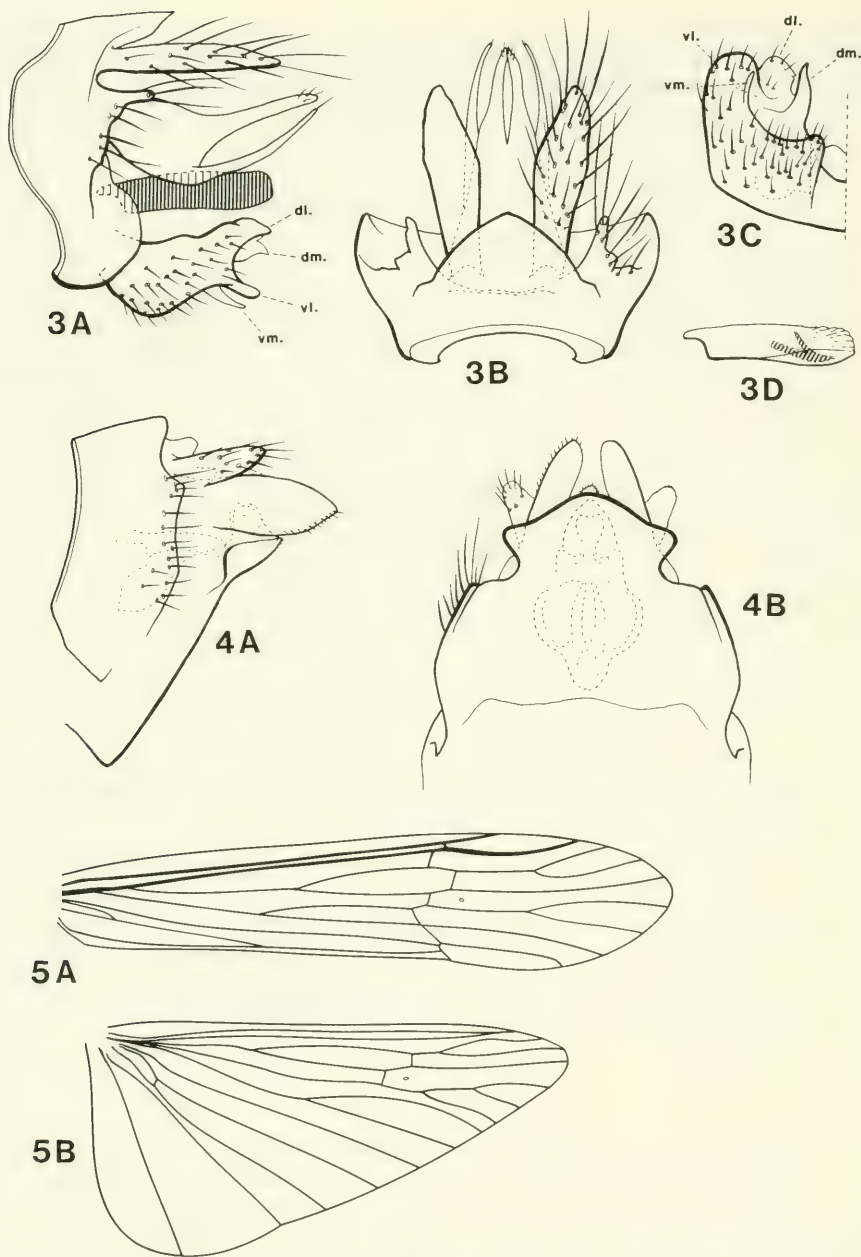
KEY TO GENERA OF NEOTROPICAL TRIPLECTIDINAE (ADULTS)

- 1. Hindwing fork III present in both sexes (i.e. M 3-branched); female forewing fork III present Triplectidinae 2
- Hindwing fork III absent in both sexes (i.e. M 2-branched); female forewing fork III absent (except in *Amphoropsyche*, where it is present) ... Leptocerinae
- 2. Forewing thyridial cell very long and slender, almost twice as long as discal cell 3
- Forewing thyridial and discal cells subequal in length 4
- 3. Hindwing crossveins *rs* and *r-m* in line and fork I very narrow or absent; male inferior appendage without basoventral lobe or 2nd article *Notalina* (*Neonotalina*) Holzenthal
- Hindwing crossvein *rs* apicad of *r-m* by at least its length and fork I, when present, not particularly narrow; male inferior appendage with basoventral lobe and 2nd article *Triplectides* Kolenati
- 4. Tibial spurs 2,2,4 *Hudsonema flaminii* (Navás)
- Tibial spurs 0,2,2 5
- 5. Frontal setal wart long, narrow; 2nd article of male inferior appendage well developed, $\frac{1}{2}$ –1 $\times$ as long as apicodorsal portion of 1st article; male abdominal segment X without apical, digitate processes; female segment X without thin, ventrally directed, sclerotized plate below appendages of X *Grumichella* Müller
- Frontal setal wart oval; 2nd article of male inferior appendage underdeveloped, less than $\frac{1}{4}$ as long as apicodorsal portion of 1st article; male abdominal segment X with 2 pairs of apical, usually digitate, processes; female segment X with thin, ventrally directed, sclerotized plate below appendages of X *Atanatolica* Mosely

EVOLUTION

Ulmer (1906, 1907) first divided Leptoceridae into its two subfamilies Triplectidinae and Leptocerinae based on whether the discal cell of the hindwing is closed or open, respectively. Morse (1981) inferred monophyly for Triplectidinae by the synapomorphic absence of the primitive phallic parameres and vestigial phallicata (“aedeagus” of Nielsen, 1957); evidence for monophyly for Leptocerinae was indicated by the absences of one branch of the median vein (“Fork 3”) and of the sectoral vein (“open discal cell”) in the hindwing and the lack of preapical spurs on the mesothoracic tibiae.

Morse (1981) further identified three tribes of Triplectidinae: Grumichellini, Hudsonemini, and Triplectidini. Monophyly for Grumichellini was supported by absences of apical spurs on the prothoracic tibiae and preapical spurs on the meso- and metathoracic tibiae; for Hudsonemini, by the broad vertical plates of the phallotremal sclerite; and for Triplectidini, by the possession of an extra appendage



Figs. 3-5. *Hudsonema flaminii* (Navás). 3, Male genitalia. A, Lateral. B, Dorsal. C, Left inferior appendage, ventral. D, Phallic apparatus, lateral. 4, Female genitalia. A, Lateral. B, Ventral. 5, Male wings. A, Forewing. B, Hindwing.

articulating with the base of each inferior appendage. The historical relationships of the three tribes among themselves were left unresolved.

Morse (1981) placed *Hudsonema*, *Condocerus*, *Notalina*, and *Triplexa* in the Hudsonemini. However, *Triplexa* shares several unique genitalic and venational characters with the grumichelline genera *Atanatolica* and *Grumichella* (Holzen-

thal, unpublished) and is here removed from Hudsonemini and transferred to Grumichellini. Discovery of the immature stages of *Triplexa* possibly will test this phylogenetic hypothesis since known Grumichellini immature stages are highly derived, with several striking homologues.

Monophyly for the Hudsonemini is therefore supported by the following homologues (Fig. 6): (1) phallotermal sclerite with vertical extensions (Morse, 1981, fig. 2; Fig. 3D), (2) presence of secondary setae on lateral sclerite of each anal proleg (Fig. 1E; cf. Williams and Wiggins, 1981), and (3) absence (or fusion of vestige) of the 2nd article of each inferior appendage. The ventromesal spine on each inferior appendage of *Notalina* species (Holzenthal, 1986) and the ventromesal or dorsomesal spine on each inferior appendage of *H. flaminii* (Figs. 3A, 3C) may be the fused vestige of this 2nd article.

Within the Hudsonemini, the homologue which provides evidence for the monophyly of *Notalina* is (Fig. 6): (4) fork I of the hindwing very narrow, with a tendency to become lost. *Condoceris* and *Hudsonema* appear to be sister lineages because of: (5) shared possession of short, compact inferior appendages. Monophyly for the two species of *Condoceris* is supported by the following inferred homologues in the male genitalia: (6) abdominal segment IX "L"-shaped, broadest ventrally at point of insertion of inferior appendages; (7) inflected, spinose apices and (8) short, broad, triangular mesal lobes of the inferior appendages (Neboiss, 1977, figs. 747, 752).

There is no clear evidence for the monophyly of the three species of *Hudsonema*. Homologues are not evident in adult genitalia because of the obscuring effects of striking autapomorphies in *H. flaminii*. The pattern of setae and setal-bearing sclerites on the larvae of each of the three species is identical (Figs. 1A, 1B, 1E, 2A; Cowley, 1978, figs. 45, 46), except that in the New Zealand species metanotal *sa2* sclerites are absent. For example, larvae of all three species have a transverse row of numerous secondary setae on their metasterna; all have very similar lateral hump sclerites on abdominal segment I; and all have virtually identical terminal abdominal sclerites. Unfortunately, larval chaetotaxy of the Leptoceridae and related families has not been investigated to determine which conditions of setae and sclerites are part of their groundplan and which are derived from it. Thus, although together these phenetic characters distinguish *Hudsonema* larvae from related genera, they are not understood adequately to support monophyly. Taking the conservative taxonomic approach, therefore, *H. flaminii* is left as a species of *Hudsonema*, rather than transferred to *Condoceris* or to a new monotypic genus, on the supposition that: (9) one or more of the above phenotypic larval similarities will eventually be corroborated as homologues.

Hudsonema aliena and *H. amabilis* are considered to be sister species based on (Fig. 6): (10) very short, broad preanal appendages and (11) long, slender apicolateral extensions of the phallobase in the male genitalia (Mosely and Kimmins, 1953, figs. 165, 167).

HISTORICAL BIOGEOGRAPHY

Triplectidinae are restricted to Australasia and the Neotropics; the subfamily Leptocerinae is cosmopolitan. Morse (1981) hypothesized that the Triplectidinae arose via vicariance as the South American-Antarctic-Australian landmass rifted from the rest of Gondwanaland 130–85 myBP.

Craw (1979, 1982) presented evidence indicating that the well-documented

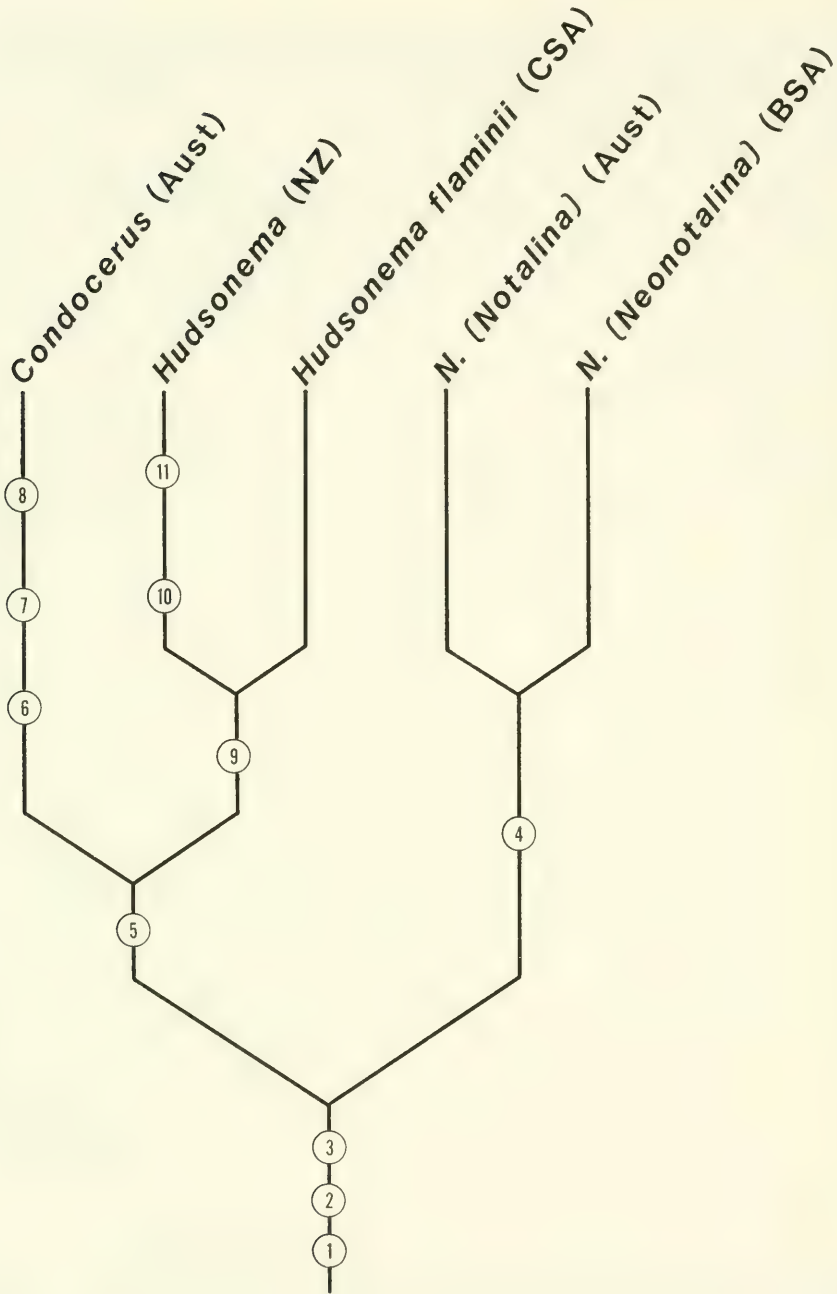


Fig. 6. Phylogeny of the genera of Hudsonemini.

trans-Antarctic distribution pattern is composed of two distinct biogeographical tracks: an Australian-South American track and a New Zealand-South American track. Many New Zealand and Chilean South American taxa are more closely related to each other than to Australian sister taxa. Caddisflies exhibiting this pattern include, in the Helicophidae, *Alloecentrella* (New Zealand) and *Alloecen-*

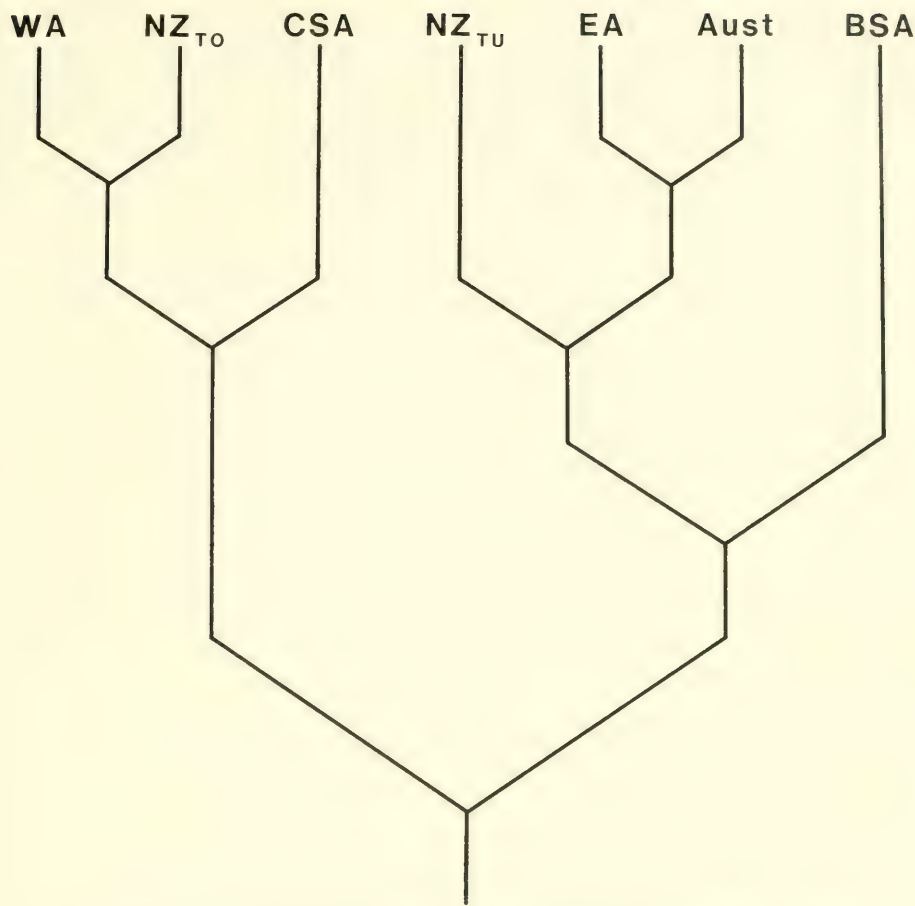


Fig. 7 Breakup of a section of Gondwanaland (adopted from 'Craw 1979, 1982, 1983).

trellodes (Chile) (Flint, 1979) and, in the Kokiriidae, *Kokiria* (New Zealand) and *Rhynchopsyche* (Chile) (Cowley, 1978). As indicated by the phylogeny discussed above, *Hudsonema* has two species in New Zealand (widely distributed and sympatric on both North and South Islands) and one species in Chilean South America. Its sister genus *Condocerus*, with two described species, is distributed in south-western Western Australia, Victoria, and Tasmania.

Craw (1982, 1983; see also Platnick and Nelson, 1984) constructed a model of Pacific biogeography (Fig. 7) in which his Torlese terrane New Zealand (NZ_{TO}) was associated with Western Antarctica (WA) and Chilean South America (CSA). His Tuhua terrane New Zealand (NZ_{TU}) was associated with the eastern margin of the Australian plate (Aust) and East Antarctica (EA). This latter landmass had connections with Brazilian South America (BSA). NZ_{TO}-WA-CSA apparently separated from NZ_{TU}-EA-Aust-BSA during mid-Cretaceous times. This possibly resulted in the vicariant origins of *Hudsonema* and *Condocerus* populations on the former and latter landmasses, respectively, from a triplectidine ancestor primitively distributed over both. The model predicts that *Condocerus* species should occur in BSA and NZ_{TU}. The fact that such species are not known from these

regions may be due to extinction, but more likely, at least for BSA, is the result of an inadequately inventoried fauna; species of *Notalina* (*Neonotalina*), for instance, were recorded and described from the BSA Neotropics only very recently (Holzenthal, 1986). Subsequent separation of CSA from NZ_{TO}-WA and the former micro-continent's migration to its present association with BSA resulted in the present day disjunction seen in the distribution of *Hudsonema*. Sympatry of two of the *Hudsonema* species throughout New Zealand today is probably the result of recent dispersals.

Triplectidines exhibiting an Australian-South American trans-Antarctic track were possibly represented by an ancestral biota distributed over NZ_{TU}-EA-Aust-BSA that vicariated when BSA separated from NZ_{TU}-EA-Aust. Caddisfly relationships and distributions conforming to the latter scenario include species in *Notalina* and Grumichellini (here including *Triplexa*). Interestingly, Neotropical *Notalina* (*Neonotalina*) and the two Neotropical grumichellines, *Atanatolica* and *Grumichella*, are only known to occur today in BSA. These taxa may be descendants of a distinct, tropical component of the trans-Antarctic biota, traditionally accepted to have been temperate in nature (Cracraft, 1975). *Triplectides* species, although not yet analyzed phylogenetically, may conform to both Australian-South American and New Zealand-South American trans-Antarctic tracks; the genus has species in both BSA and CSA as well as Australia and New Zealand.

The phylogeny of the genera of Hudsonemini and, especially, the species of *Hudsonema*, presented above, is based upon few apparent homologues. That phylogeny (and the biogeographic interpretations based upon it), like all scientific hypotheses, is subject to further corroboration or falsification. Properly formulated, though, phylogenetic and vicariance hypotheses can be used to predict geographic and evolutionary patterns for as yet undiscovered or unstudied taxa (Morse and White, 1979; Savage, 1982). The geographic and evolutionary relationships of southern long-horned caddisflies support the predictions of Craw's model of Pacific biogeography as well as his contention that the trans-Antarctic distribution is a composite of at least two distinct biogeographical tracks.

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DISCOVERY OF THE IMMATURE STAGES OF
PARASIMULIUM CROSSKEYI PETERSON (DIPTERA: SIMULIIDAE),
WITH A DISCUSSION OF A UNIQUE BLACK FLY HABITAT

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Abstract.—Larvae, pupae, and teneral adults of *Parasimulium crosskeyi* Peterson were collected in June 1984 from a hyporheic habitat adjacent to Wahkeena Creek, Oregon. An account of the collection and brief description of larvae and pupae are given. The immature stages of *Parasimulium* appear to be obligate members of the hyporheic zone. Morphology reveals a number of similarities with typical cavernicolous organisms, including apparent blindness of larvae and reduced cuticular pigmentation in both larvae and pupae. In addition to suspension feeding, larvae may be consuming organic detritus deposited in the substrate.

Dipterists have been interested in the enigmatic black fly genus *Parasimulium* Malloch, since the initial collection of adults over 70 years ago. Until recently, only eight male specimens were available for study, all but one collected by A. L. Melander in the Pacific Northwest (Washington, Oregon, and northern California). Included were the type species, *Parasimulium furcatum* Malloch, and a single representative of *Parasimulium melanderi* Stone. Peterson (1977), in a review of the genus, assigned the latter specimen to a new subgenus, *Astoneomyia*, and described two new species, *Parasimulium* (P.) *stonei* and *Parasimulium* (P.) *crosskeyi*, from the remaining material. In 1981, D. M. Wood and A. Borkent revisited the type locality of *P. crosskeyi* (Benson Park, Multnomah Co., Oregon), and collected large numbers of this presumed rare black fly at adjacent Wahkeena Creek (Wood and Borkent, 1982). Their findings included discovery of the first females, and detailed information on behaviour of adults. Subsequently, additional information has been gathered for *P. crosskeyi*, and *P. stonei* (Peterson and Courtney, 1985; Borkent and Wood, 1986).

The papers by Peterson (1977) and Wood and Borkent (1982) have fostered considerable interest in locating larvae and pupae of *Parasimulium*. Because immature black flies possess a number of phylogenetically significant characters, discovery of these stages is a prerequisite to clarifying the position of *Parasimulium* within the Simuliidae.

Larvae, pupae, and teneral adults of *P. crosskeyi* Peterson were found in the hyporheic zone adjacent to Wahkeena Creek, Oregon (45°34'N, 122°07'W). The following is an account of the collection, a brief description of larvae and pupae, and discussion of ecological and phylogenetic considerations.

OBSERVATIONS AND COLLECTIONS

Wahkeena Creek was visited on several occasions during 1984. *Parasimulium crosskeyi* adults were seen from May 26 to July 7, but abundances on these dates suggest that the period of activity is actually longer. Adults were most abundant during the first two weeks in June, and this may represent peak emergence time. Hundreds of *Parasimulium* adults were observed on June 11–12, primarily along the creek between the scenic highway and the southern border of Benson Park (Wood and Borkent's "section 4"). Behaviour of adults was as described by Wood and Borkent (1982), with males hovering or resting beneath leaves of bigleaf maple, *Acer macrophyllum* Pursh, red alder, *Alnus rubra* Bong., and other streamside vegetation. Adult black fly numbers were greatest at trees overhanging Wahkeena Creek, but some individuals were observed beneath *Acer* as far as 50 m from the stream. Flight times on June 11–12 generally agreed with Wood and Borkent's findings, with adults active from 0630 h to 2100 h. Male *Parasimulium* were found resting beneath the leaves of streamside vegetation long after sunset (ca. 2200 h).

At approximately 1200 h on June 12, large numbers of adult *P. crosskeyi* were observed near a seep below the Wahkeena Creek picnic area. The seep drains a seemingly large hyporheic zone (interstitial aquatic habitats below and lateral to the streambed) beneath the park, with Wahkeena Creek the ultimate source of water for the habitat. Water from the creek apparently percolates through coarse substrates lateral to the streambed, and continues via subterranean passageways under the picnic area. Water leaving the hyporheic zone drains into a shallow pool and re-enters Wahkeena Creek ca. 10 m from the seep. A variety of herbaceous plants, including stinging nettle, *Urtica dioica* L., bracken fern, *Pteridium aquilinum* (L.) Kuhn., and horsetail, *Equisetum telmateia* Ehrh., surrounded the seep outlet. Because *P. crosskeyi* adults were swarming beneath these low-lying herbaceous plants, instead of the typical woody trees and shrubs, the site appeared unique, and warranted further investigation.

The outlet of the hyporheic zone was excavated in hopes of finding the immature stages of *P. crosskeyi*. The habitat contained coarse substrates, primarily cobble-sized (sensu Cummins and Lauff, 1969) stones, which provided an extensive interstitial network, both below and above the water level. While rocks were removed from the seep, a net was held downstream to collect dislodged material. The current carried large amounts of woody and root-derived detritus out of the seep, and the net required periodic cleaning. Several trays of debris were checked for immature black flies, but only *Prosimulium esselbaughi* Sommerman were seen. However, each tray contained 1–2 teneral adult *P. crosskeyi*, which seemed to emerge from within the detritus. Because of the abundance of adults near the seep outlet, and the possibility of external contamination of samples, extreme care was exercised in collecting the last, and deepest (ca. 1 m into bank) sample. The sample contained no visible immature black flies, but did include 5 teneral adults. A close sex ratio of all "hyporheic" adults (2 males: 1 female), relative to samples taken elsewhere (ca. 10% females), was additional evidence that the site was unique. Debris from the last sample was retained for laboratory examination, in hopes of finding pupal exuviae of collected adults. This proved successful, as numerous exuviae, 2 male pupae, and 3 larvae of *P. crosskeyi* were found. As-

sociation of pupae was by examination of the pharate adult through the pupal integument; genitalia were well developed and assignable to *P. crosskeyi*. Larvae possessed poorly developed gill histoblasts, so association with pupae was not possible; however, structure of the hypostoma was unusual, and resembled that of early instar *Parasimulium* larvae reared from eggs (Borkent and Wood, 1986).

DESCRIPTION OF IMMATURE STAGES

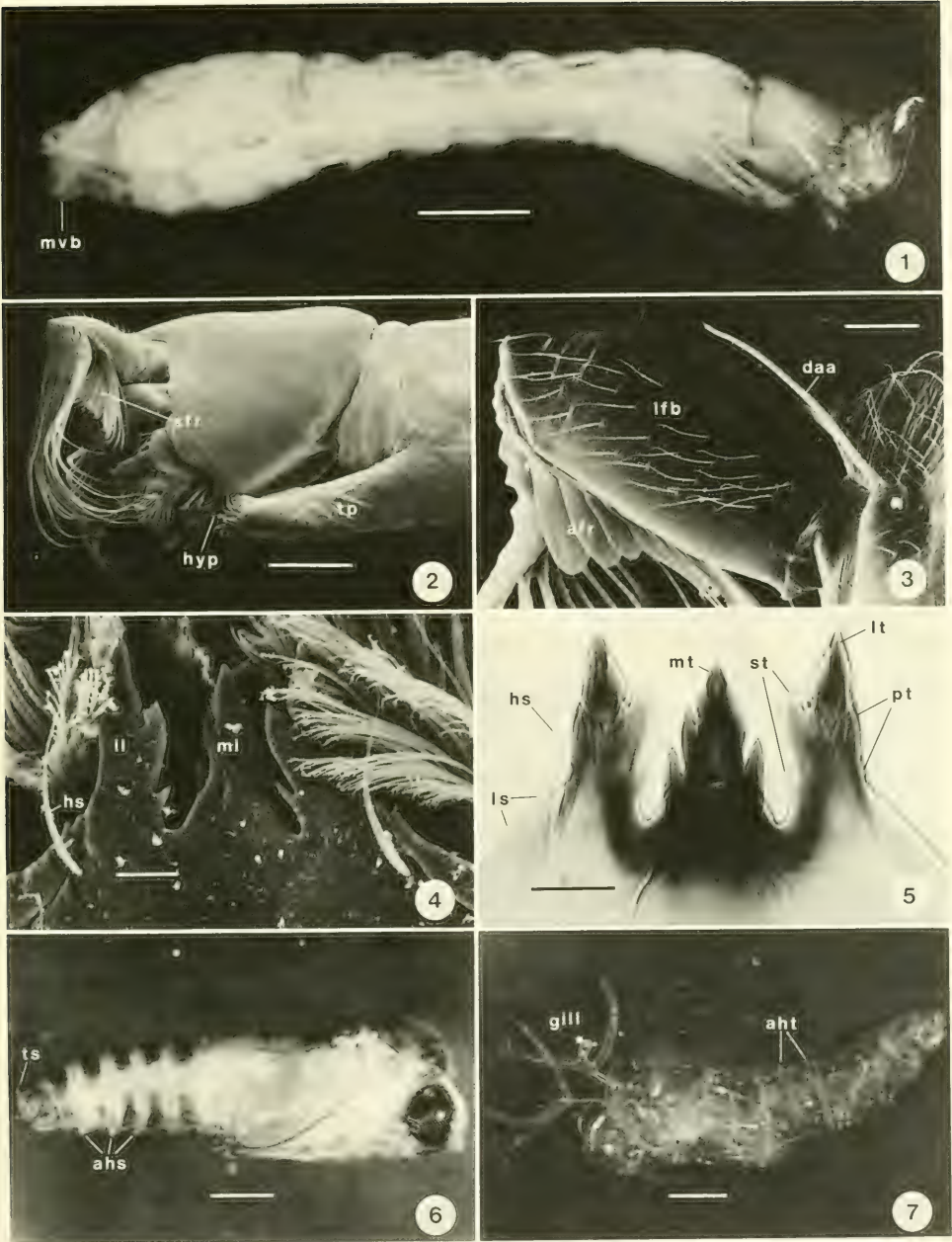
A full description of *P. crosskeyi* larvae and pupae awaits collection of additional material, particularly last instar larvae. I therefore present only a general description of the more salient features of collected specimens, with emphasis on characters that may be of phylogenetic importance.

Numerous larvae have been examined (including additional specimens collected at Wahkeena Creek on January 5, April 19, May 16, June 10, and June 24, 1985). Total length from 1–5 mm, with the latter probably representing the penultimate or antepenultimate instar. Cuticle is unpigmented, except for a few heavily sclerotized structures on the head (Fig. 1); stemmata not apparent. Labral fans well developed (Fig. 2); secondary fan rays as in *Prosimulium*, with tips arranged in a straight line. Antenna relatively short, extending to ca. $\frac{3}{4}$ length of labral fan base; proximal and medial articles (sensu Currie, in press) short, with distal article comprising 80% of antennal length (Fig. 3). Hypostoma (Figs. 4, 5) with 3 distinct lobes; lateral lobe with pronounced apical (lateral) tooth, 2 sublateral teeth (with innermost tooth small, and outermost tooth large), 2 small paralateral teeth, and 5 or more lateral serrations; median lobe slightly less pronounced than lateral lobes, and separated from lateral lobes by deep slots; median lobe with apical tooth and 3 lateral tines, which, beginning on the posterior right margin, alternate to the apex; margins of apical median, lateral, and outermost sublateral teeth serrated. Postocciput nearly complete, enclosing cervical sclerites. Postgenal cleft moderately shallow, but visible only after staining. Thoracic proleg elongate, its apex extending to a point anterior to the hypostomal groove. Abdomen with pronounced mid-ventral bulge (Fig. 1). Gut contents of one specimen included coarse sand grains, leaf particles, and a larval chironomid head capsule.

Two male pupae and several pupal exuviae were examined. Total length from 2–3.5 mm. Pupal integument transparent (Figs. 6, 7). Gill filaments translucent, inflated and with shallow annulations; gill consists of an elongate base and two strongly divergent primary trunks; dorsal trunk simple and ventral trunk branching horizontally into two filaments of subequal length. Abdominal tergites 3 and 4, each with 8 anteriorly-directed hooks along posterior margin. Tergite 9 with a pair of curved, moderately long, dorsally-directed terminal spines. Posterior margins of abdominal sternites 5–7, each with 2 anteriorly-directed hooks, situated on postero-ventrally directed tubercles. Cocoon a thinly-woven sack covering the abdomen and thorax, with a poorly defined anterior margin.

DISCUSSION

Hyporheic insect faunas are well documented (see Hynes, 1983; Williams, 1984) and include a variety of Diptera, Ephemeroptera, and Plecoptera. Some taxa are considered obligate members of the subterranean community (Stanford and Gausfin, 1974), but most are transient, remaining in the hyporheos only until reaching a larger, presumably less vulnerable, size. The habitat is therefore dominated by early instars of typical surface benthos. Black flies are rarely included in discussions



Figs. 1-7. *Parasimulium crosskeyi*. 1, Photomicrograph of whole larva, showing mid-ventral bulge (mvp). Scale = .5 mm. 2, Scanning electron micrograph of larval head and anterior thorax, showing secondary fan rays (sfr), hypostoma (hyp) and thoracic proleg (tp). Scale = .2 mm. 3, Scanning electron micrograph, showing labral fan base (lfb) and larval antenna (distal article = daa). Scale = 50 μ m. 4, Scanning electron micrograph of larval hypostoma, showing hypostomal sensillum (hs), lateral lobe (ll) and median lobe (ml). Scale = 20 μ m. 5, Photomicrograph of larval hypostoma, showing lateral serrations (ls), hypostomal sensillum (hs), median tooth (mt), sublateral teeth (st), lateral tooth (lt) and paralateral teeth (pt). Scale = 20 μ m. 6, Photomicrograph of male pupa (gills absent), showing terminal spines (ts) and recurved abdominal hooks on sternites 5-7 (ahs). Scale = .5 mm. 7, Photomicrograph of pupal exuvia showing gill and location of recurved abdominal hooks on tergites 3-4 (aht). Scale = .5 mm.

of hyporheic environments, mostly because of rather conservative views about larval feeding habits. Simuliids are usually considered strict suspension feeders and, to a lesser degree, scrapers of attached periphyton. In fact, larvae are generally capable of engaging in several feeding strategies, depending on food resources (Currie and Craig, in press).

A number of simuliids are facultatively hyporheic. Peterson (1970) reported that *Prosimulium onychodactylum* Dyar and Shannon [complex] often pupates within gravels of the stream bottom. He also predicted this behaviour for *P. susanae* Peterson, which has been corroborated under laboratory conditions (D. A. Craig, unpubl. data). These examples pertain to stationary, non-feeding stages, and entrance into the hyporheic zone may accrue only defensive advantages. Black fly larvae entering this environment may have to cope with dramatically different food resources than in surface habitats. Larvae of *Gymnopaia* Stone, scrapers inhabiting small, arctic-alpine streams, are capable of surviving in the hyporheos (Currie and Craig, in press). The organism retreats into the substrate during periods of excessive or low flow, and apparently becomes a detritivore. Early instar *Gymnopaia* larvae are uncommon in surface samples, but may frequent the hyporheic zone, even during normal flow conditions (D. C. Currie, pers. comm.). Collections at Wahkeena Creek indicate that *Simulium pugetense* (Dyar and Shannon) [complex] (collected in January, April, and May 1985) and *Prosimulium esselbaughi* may enter the hyporheic zone. The presence of these suspension-feeding larvae in the Wahkeena Creek hyporheos may reflect the site's unique characteristics. The poorly-sorted, coarse substrate and extensive interstitial network probably allow surface benthos easy access into the subterranean habitat. Future research may uncover additional simuliid taxa, the larvae of which are capable of surviving in similar hyporheic environments.

Unlike the above simuliids, *Parasimulium* appears to be an obligate member of the hyporheic zone. Morphology of the immature stages of *P. crosskeyi* demonstrates a number of similarities with typical cavernicolous organisms (Howarth, 1983). Apparent blindness of larvae, and unpigmented cuticle in both larvae and pupae, are among these subterranean adaptations. Ecological characters seem equally affected by this life style. Period of adult emergence is somewhat protracted in *P. crosskeyi*, extending at least 5 weeks. *Parasimulium stonei* exhibits a similar pattern (Peterson and Courtney, 1985). This asynchrony of emergence could be a response to dampened environmental cues, relative to surface habitats. Wahkeena Creek is a short (<1.5 km), spring-fed system, which exhibits much less seasonality than most Pacific Northwest streams. The extended period of emergence in *P. crosskeyi* may reflect subtle changes in water temperature or chemistry; however, establishing this with certainty requires detailed examination of ecological parameters. An additional consideration pertains to food availability. The Wahkeena Creek hyporheic habitat contains an abundance of woody and root-derived organic debris. Fine particulate organic matter (FPOM) derived from this debris is a potential food for the fully-fanned *Parasimulium* larvae, provided subterranean current velocities are high enough to suspend particles in the water column. No data on underground currents is available, but relative discharge at the collection site, and adjacent seepages, and the presence of two filter-feeding simuliid taxa (*S. pugetense*, *P. esselbaughi*), suggest that flow is sufficient to maintain a fauna of suspension feeders. Although *Parasimulium* seems capable of this

feeding strategy, analysis of the gut contents of one specimen indicates that larvae may be "deposit" feeding on the microbial and invertebrate (e.g. chironomid) fauna associated with detritus. Future gut analysis of larvae, and closely monitored behavioural studies should provide valuable insights on the feeding strategies of *Parasimulium*.

The discovery of immature stages of *Parasimulium* will surely rekindle the controversy surrounding higher classification of the Simuliidae. Character analysis incorporating data on *Parasimulium* larvae and pupae will provide a test of the classification used by several authors (Crosskey, 1969; Peterson, 1977; Wood and Borkent, 1982; and others), which places *Parasimulium* in a subfamily by itself, the Parasimuliinae. Such analysis may, instead, indicate that the genus simply constitutes an aberrant prosimuliine branch. It is evident that the immature stages of *Parasimulium* and those of the Prosimuliini share a number of character states; however, many of these represent the presumed plesiomorphic condition and, as such, are of little value in reconstructing phylogenies (Wiley, 1981). In addition, ecological (e.g. habitat) specialization may distort interpretations of character polarity. Elucidating the relationship between *Parasimulium* and the rest of the Simuliidae requires a thorough phylogenetic analysis. Discovery of the immature stages of *P. crosskeyi* will provide an impetus for such examination, and foster a renewed interest in hyporheic research.

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THE FIRST AND SECOND LARVAL INSTARS AND THE EGG
OF *PARASIMULIUM STONEI* PETERSON
(DIPTERA: SIMULIIDAE)

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Abstract. — The first instar larva of *Parasimulium stonei* has only a single minute labral fan ray and apparently lacks an anteromedian palatal brush. The sensilla of the maxillary palpus are arranged laterally on its apical portion and spicules are also present. Second instar larvae have a labral fan similar in form to that of most Prosimuliini. Some of these data suggest a relationship with typical members of the Prosimuliini, thus contradicting previous suggestions, based on study of adults, of a sister group relationship with all other Simuliidae. The shape of the egg is essentially the same as that of other blackflies, triangular, with a dorsal, transverse bulge.

Rediscovery of adults of *Parasimulium crosskeyi* Peterson, nearly 50 years after the last known specimens of the genus were collected, has led to renewed interest in the genus and its phylogenetic position (Wood and Borkent, 1982) and intensified the search for immature stages. Smart (1945) erected the subfamily Parasimuliinae for this genus alone, and several subsequent authors (Crosskey, 1969; Rubtsov, 1974; Peterson, 1977) followed this arrangement. These authors put the Parasimuliinae at the beginning of their classifications, with the statement or implication that it represented the most primitive member of the family. The notion that *Parasimulium* is the most primitive simuliid was supported by Wood and Borkent (1982) who, in examining adults, postulated a sister-group relationship between *Parasimulium* and all other blackflies. Information about the immature stages would test this idea and hopefully add significantly to our understanding of the polarity of character states within Simuliidae. In this paper we describe and discuss the newly discovered first and second instar larvae of *Parasimulium stonei* Peterson and reassess our original hypothesis.

In spite of intensive searching in a variety of microhabitats in the area of Wahkeena Creek, Benson State Park, Oregon, where the adults of *P. crosskeyi* Peterson were found to be common, we were unable to locate immature stages. In May 1983 one of us (DMW) discovered male and female adults of *Parasimulium stonei* beside a small rivulet near Humboldt Redwoods State Park, Humboldt County, California and was able to obtain a few eggs from a female of this species. This female was simply placed in a transparent, plastic shell vial whose open end was closed with a piece of maple leaf. Eggs were laid in the moisture that formed on the side of the vial. These small transparent eggs were then flooded

with distilled water and placed in a refrigerator. Some of them hatched sometime during the following winter (while under refrigeration), but because of their minute size and transparency, the larvae were not discovered until after they had all died. Some of the first instar larvae had molted to the second instar. They were then preserved in 70% ethanol. These specimens formed the basis of the following description and analysis.

In this paper we follow the general morphological terms given by Teskey (1981). For specific structures, we follow those given by Craig (1974) for the labrum, by Craig and Borkent (1980) for the maxillary palpus and by Craig and Batz (1982) for the antenna and associated sensilla.

DESCRIPTION

Egg.—When first laid, the eggs of *P. stonei* were transparent but by the time of hatching had acquired a light brown pigmentation. The shape of the egg was similar to that of other blackflies, with a swollen dorsal transverse bulge (Davis, 1971) and we are not able to see any essential difference between it and the eggs of other blackflies with which we are familiar (those of species of *Gymnopaia* Stone, *Twinnia* Stone and Jamnback, *Prosimulium* Roubaud, *Simulium* Latreille). This egg shape is evidently a synapomorphic character state of the Simuliidae since the eggs of other Nematocera are either oval or nearly cylindrical in outline.

Eggs of *P. stonei* were 243–265 μm ($n = 3$) in length. Some of the eggs we observed held mature first instar larvae and in such instances the only part of the larva which could be seen was the dark egg burster on the dorsum of the head capsule.

First instar larva.—General body form typically simuliid like, with details of anterior proleg and posterior anal hooks not discernable; head capsule transparent except for black egg burster (Fig. 1a); eye spot lacking; antenna (Fig. 1c) a single article with terminal uniporous cone sensillum, two basal multiporous peg sensilla (mps) and trichoid sensillum 2 (ts2), associated bacteria-covered multiporous sensillum (bms) (no bacteria present in our specimens) (Fig. 1b) and trichoid sensillum 1 (ts1); labrum (Fig. 2a, b) with setae 5C, 6C mesal to antenna (Fig. 1b), 2C, 4C present, 3C questionably present, single labral fan ray situated laterally, about half way between setae 2C and 4C (Fig. 1d, e); anterior palatal brush apparently absent; maxillary palpus with complete complement of sensilla (Fig. 2c, d) (Craig and Borkent, 1980: Fig. 2) but 1E, 2E and G not discernable (probably too dirty), sensilla arranged laterally on apical portion of palpus and in circular configuration, spicules present (Fig. 1b); hypostoma (Fig. 2e, f) with prominent triangular median tooth, shorter lateral tooth and scarcely discernable intermediate teeth.

Second instar larva.—Similar to first instar in general body form; head capsule lacking pigmentation, except for a tiny eye spot and sclerotized hypostoma; antenna similar to first instar but basal article supporting two multiporous sensilla, more elongate; labral fan (Fig. 3a) well developed, with single, anterior, medially directed, fringed ray, behind which is a short series of rays, also directed medially, primary fan with over 10 rays, secondary triangular fan with five rays, restricted to lateral margin; mandible with apical spicules and teeth (Fig. 3d); maxillary palpus sensilla not readily interpretable (too dirty) but all arranged apically on palpus, spicules absent; hypostoma (Fig. 3e) with median tooth long, sharply

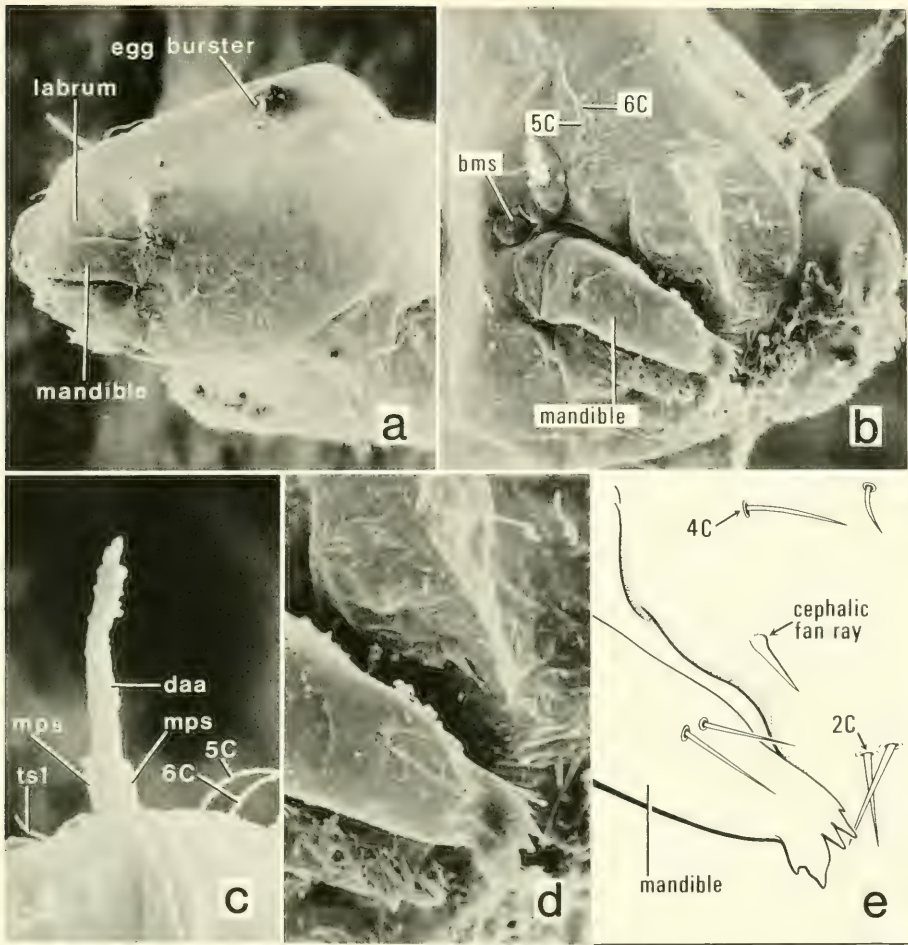


Fig. 1. First instar of *Parasimulium stonei*. a, Dorsolateral view of head capsule. b, Anterolateral view of head capsule, *bms* (bacteria-covered multiporous sensillum). c, Anterior view of right antenna, *mps* (multiporous peg sensillum), *daa* (distal antennal article), *ts1* (trichoid sensillum). d, Ventral view of right mandible and labrum. e, Drawing of figure d.

pointed, as long as broad, submedian tooth vestigial; all remaining teeth (lateral and intermediate) arising in two groups at apex of long, parallel-sided, stalk-like base.

DISCUSSION

A few of the characters described here can be interpreted from either a phylogenetic or an ecological perspective.

Courtney (1986) has discovered the larvae and pupae of *P. crosskeyi* Peterson in the hyporheic zone of Wahkeena Creek, Oregon. We assume that the immatures of *P. stonei* will be discovered in a similar microhabitat. Their presence in these subsurface creek gravels would correlate with the lack of eyespots in the larvae of *P. stonei* described above.

Some authors have argued that the virtual absence (i.e. reduction to a few

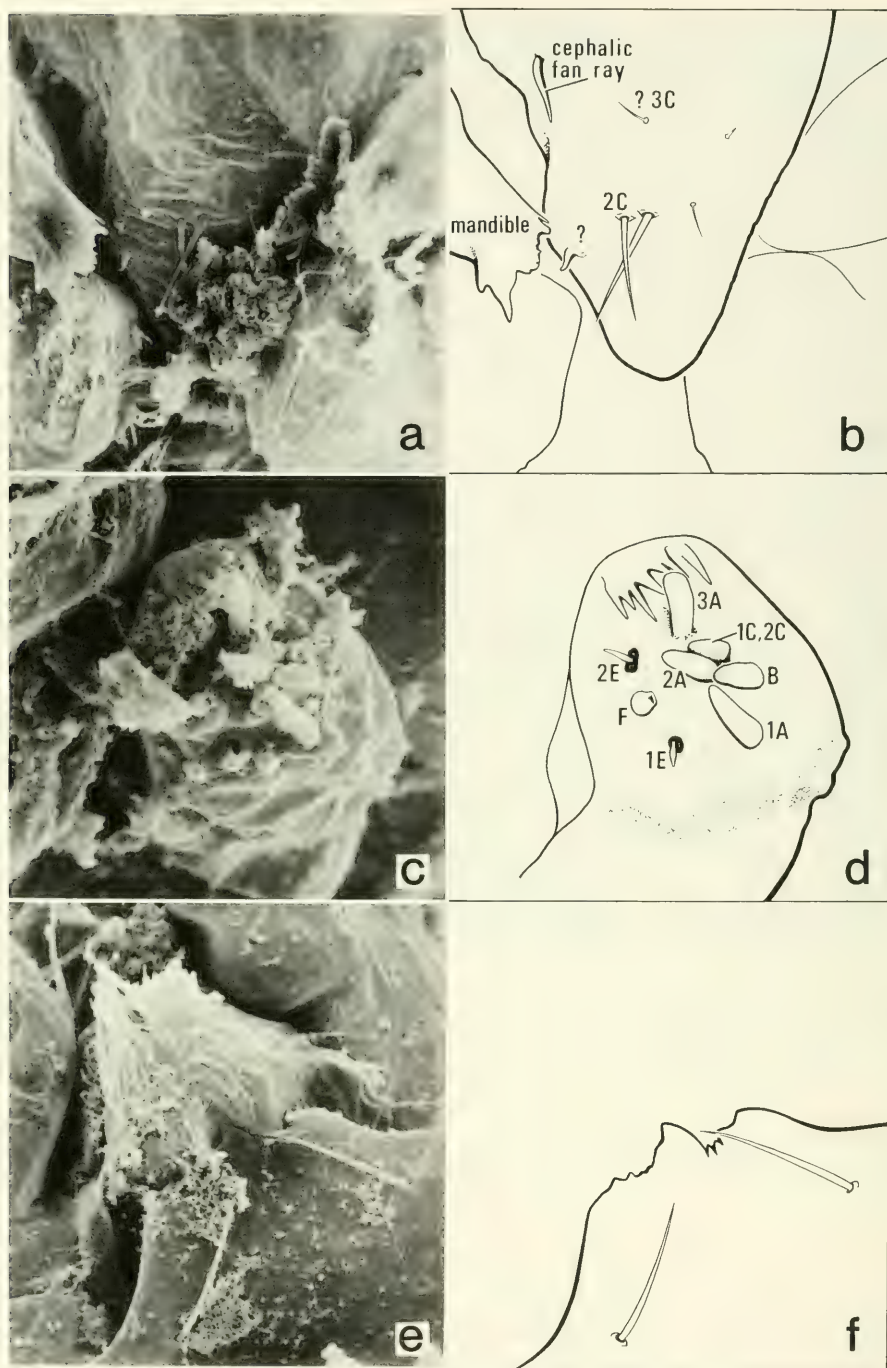


Fig. 2. First instar of *Parasimulium stonei*. a, Anterior view of labrum. b, Drawing of labrum in a. c, Ventral view of maxillary palpus. d, Drawing of palpus in c. e, Ventral view of hypostoma. f, Drawing of hypostoma in e.

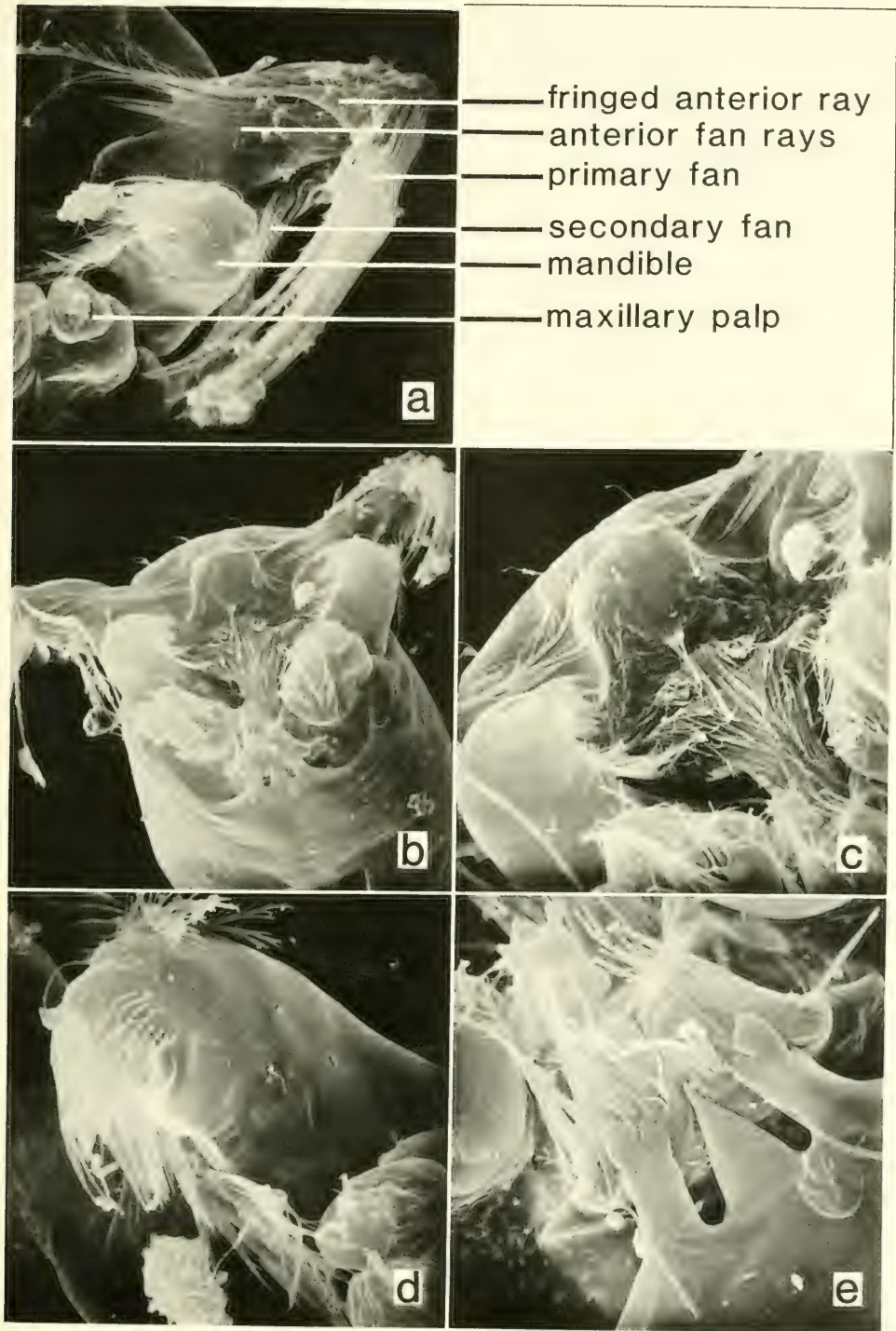


Fig. 3. Second instar of *Parasimulium stonei*. a, Ventral view of left labral fan. b, Anteroventral view of mouthparts. c, Ventral view of labrum. d, Ventral view of left mandible. e, Ventral view of hypostoma.

minute fan rays) of labral fans in first instar *Prosimulium*, and in all instars of *Gymnopsais* and *Twinnia*, is the plesiomorphic condition in the Simuliidae (Davies, 1960, 1965; Rubtzov, 1974). Craig (1974) and Wood (1978), however, have argued that the lack of fans must be considered apomorphic. Cladistically closely related families (Culicidae, Dixidae, Ptychopteridae) possess well developed homologous labral fans in each instar. Such comparisons strongly suggest that greatly reduced labral fans of some first instar larval simuliids must be considered apomorphic. First instars of *Parasimulium* share this character state with some other members of the Prosimuliini, viz, *Prosimulium*, *Gymnopsais*, *Twinnia*, and *Crozetia* (Craig, 1974), suggesting that all these genera form a monophyletic group within Prosimuliini (Figs. 4A, 5). Not all members of Prosimuliini (sensu Crosskey) lack labral fans in the first instar; those of at least one species of *Gigantodax* and one of the Australian species assigned to *Cnephia*, possess fans of normal development for first instars, showing that the Prosimuliini cannot be defined on the basis of this character state. A more detailed understanding of the distribution of this character state would be of fundamental interest in the phylogenetic interpretation of simuliids.

First instars of *Prosimulium*, *Gymnopsais*, and *Twinnia* also have paired series of scoop-shaped, apically fringed, anteromedian palatal brushes (Fig. 4A, from Craig, 1974). Such modifications of the anteromedian palatal brushes in the first instar are not known in any outgroup, and probably represent a synapomorphy of the three genera. Unfortunately, many genera remain to be surveyed for this character state. These brushes appeared to be absent in our specimen of *Parasimulium*. If they are present but not visible in our material, they are not as closely associated with seta 2C as they are in *Twinnia* (Craig, 1974: fig. 25). It will be important to determine, with the help of better specimens, whether these brushes are as highly modified in *Parasimulium* as they are in the other three genera; if they are it would be another synapomorphy linking *Parasimulium* to this group of genera.

The secondary labral fan, present in almost all simuliids that have labral fans (it is apparently absent in *Crozetia*), is shorter and smaller than the primary fan, and arises ventral to it (Figs. 3a, 4B). Rays forming the secondary fan are merely a continuation of the circle of rays that form the primary fan, separated from the last ventrolateral primary ray by a short section of aborted rays that resemble lamellae. The most proximal ray forms the anterior, or leading, edge of the secondary fan, while the most distal of the secondary rays forms the posterior edge. Our studies of the shape and arrangement of the fan rays of the secondary labral fan of various simuliids have shown that there are two discrete types of secondary fan, differing in the number and curvature of the rays (Wood et al., 1963). Crosskey (1969) pointed out that some members of his tribe Prosimuliini had a subtriangular flattened secondary fan, in which the rays were rather broad and blade-like (Fig. 4B, *Prosimulium*), and in which the apices of the fan formed a rather straight line parallel to the fan stalk. The secondary fan thus closes the space between the base of the stalk and the primary fan. In contrast, in all members of his Simuliini the secondary fan is cup-shaped and consists of finer, much more numerous, curved rays, the whole fitting within the contours of the primary fan (Fig. 4B, *Simulium*).

We have found the first type of secondary fan in the second instar of *Parasi-*

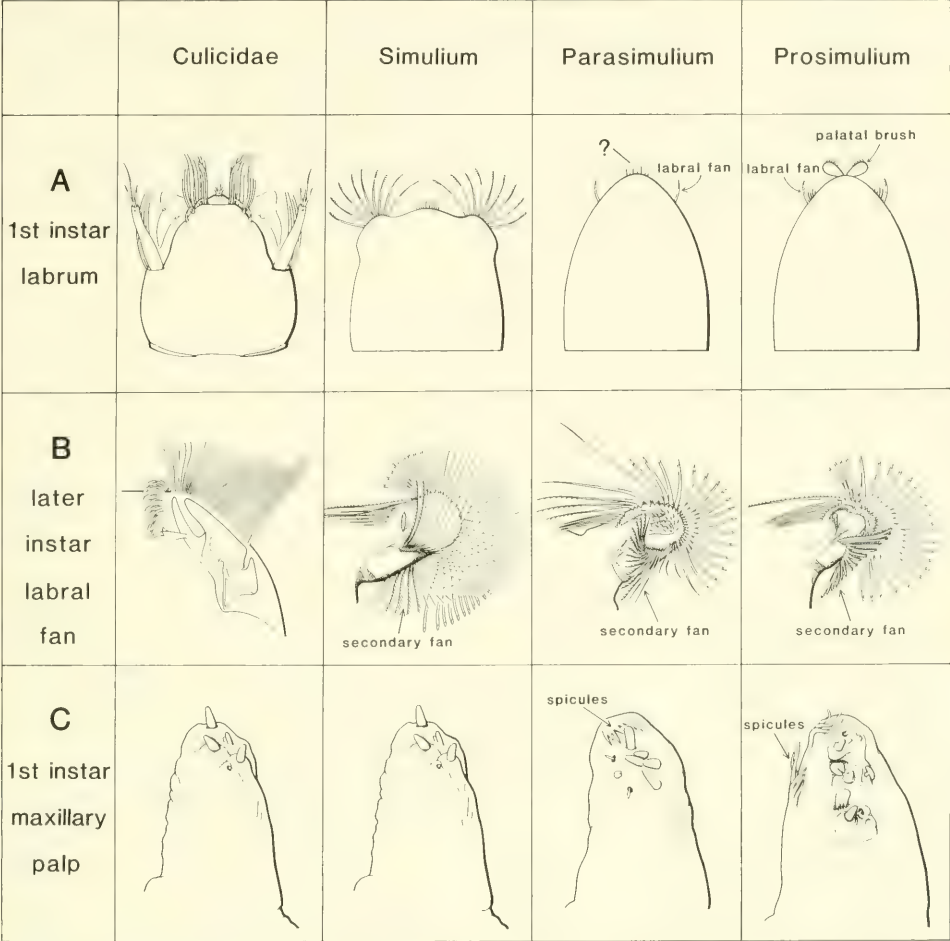


Fig. 4. Schematic representation of transformation series of character states within the Simuliidae and outgroup (as represented by Culicidae). Transformation A is partially taken from Craig, 1974.

mulium stonei; although containing more rays than that of the species of *Prosimulium* we examined, the shape of the fan is flattened and triangular, and the line formed by the apices of the fan is straight and oriented parallel to the fan stalk. We have examined various species of other genera and found the same type of arrangement. These were: several Australian species still assigned to *Cnephia* (but undoubtedly belonging elsewhere), viz., *aurantiacum* Tonnoir, *fusciflava* Mackerras and Mackerras, *orientalis* Mackerras and Mackerras, *strenua* Mackerras and Mackerras, and *tonnoiri* Drummond; several neotropical species, *Cnesia dissimilis* (Edwards), *Araucnephia montana* (Phillipi) and several species of *Gigantodax* Enderlein; and the Afrotropical *Prosimulium morotoense* McCrae and Prentice. The condition in the remaining Australian species of “*Cnephia*,” of Afrotropical *Prosimulium*, and of the other neotropical Prosimuliini remains to be determined. The secondary fan of *Ectemnia taeniatifrons* Enderlein also appeared to be of this type but was folded up in all our specimens.

The second type, with a cup-shaped secondary fan, was found in all members of *Simulium* and *Austrosimulium* examined, which Crosskey placed in his Simuliini, but was also found in some of his Prosimuliini, e.g. *Cnephia sensu stricto*, *Metacnephia*, and *Stegopterna*.

Wood (in prep) suggests that the cup-shaped second type of secondary fan is a derived condition within the Simuliidae. The presence of a subtriangular secondary fan in *Parasimulium* and some Prosimuliini must therefore be considered a symplesiomorphy and cannot be used to elucidate the phylogenetic position of the genus.

Craig and Borkent (1980) provided a comparative morphological analysis of the maxillary palpus of larval blackflies and some other nematocerous Diptera. The results showed that in nearly all taxa examined the sensilla were in a circular arrangement at the apex of the palpus. The first instars of the species of *Prosimulium*, *Gymnopais* and *Twinnia* studied were unique in having the sensilla positioned, first of all, laterally on the palpus and secondly, in a linear arrangement. The palpal sensilla of *Parasimulium stonei* are arranged laterally on the palpus but retain the plesiomorphic condition of being more or less in a circular configuration (Fig. 4C). These data also suggest that *Parasimulium* is the sister group to *Prosimulium* plus *Gymnopais* plus *Twinnia*.

Craig and Borkent (1980) also noted that there were sclerotized plates surrounding the apical sensilla of the maxillary palp of later instars of *Prosimulium*, *Gymnopais* and *Twinnia*. Among these plates were spicules that were unique to these three genera and which were therefore considered to be a synapomorphy. Of the first instar larvae of these three genera, only *Prosimulium* and *Gymnopais* had the spicules and they were lacking in those of *Twinnia*. First instar *Parasimulium stonei* exhibit the spicules, but these appear to be lacking in the second instar. In our scheme here, we suggest that the spicules are a synapomorphy of all four genera but that they have been secondarily lost in the first instar of *Twinnia*. The character state transformation is summarized in Fig. 4C.

Based on their study of adult structures, Wood and Borkent (1982) provided three character states which indicated the monophyly of Simuliidae, exclusive of *Parasimulium*. These were: (1) male eye divided by a line of discontinuity into large upper facets and small lower facets; (2) branches of radial sector (R_{2+3} and R_{4+5}) closely approximated (more widely separated in *Parasimulium*); and (3) sternite 10 of female divided medially (undivided in *Parasimulium* and other Culicomorpha). The genus *Parasimulium* was therefore considered the sister group to all other blackflies.

As discussed above, information from the first instar larvae indicates that *Parasimulium* may be the sister group to a monophyletic assemblage containing *Prosimulium* plus *Gymnopais* plus *Twinnia*. Wood (1978) has analyzed the relationship between *Prosimulium*, *Gymnopais* and *Twinnia*. Our evidence further suggests that *Crozetia* is the sister group to this assemblage of four genera (Fig. 5).

We are presently unsure of how to interpret these conflicting synapomorphies between the adults and larvae, although our inclination is to put greater weight on the larval characters. We know that divided adult eyes is susceptible to homoplasy (present also in male Bibionidae and both sexes of Axymyiidae), and that wing venation may be a poor indicator of relationship, especially considering the small difference between *Parasimulium* and *Prosimulium*. Interpretation of

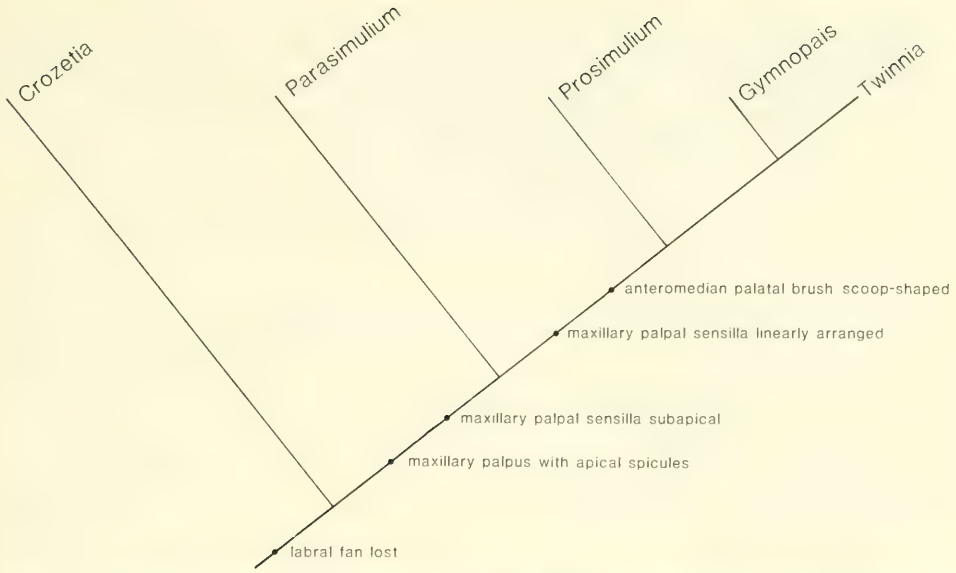


Fig. 5. Cladogram showing relationship of *Parasimulium* to some Prosimuliini. Character states are those of the first instar larva.

the incompletely divided sternite 10 of the female of *Parasimulium* remains a difficult problem as there is little doubt of the completely divided nature of the sternite in other Simuliidae contrasting with a complete sternite in the outgroup families. Although we cannot confidently resolve the present conflict, we trust that further study of other characters and their distribution will help to shed some light.

Our present analysis was possible only because of some comparative morphological studies carried out by previous workers (Craig, 1974; Craig and Borkent, 1980). While we applaud the availability of such investigations we also regret the lack of comparable studies of other structures such as the antennae, mandible and hypostoma. We hope that future work will allow the interpretation of such characters as we have described here.

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**TARSONEMUS (ACARINA: TARSONEMIDAE) MITES PHORETIC ON
THE SOUTHERN PINE BEETLE (COLEOPTERA: SCOLYTIDAE):
ATTACHMENT SITES AND NUMBERS OF BLUESTAIN
(ASCOMYCETES: OPHIOSTOMATACEAE)
ASCOSPORES CARRIED**

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Abstract. — *Tarsonemus ips* and *Tarsonemus krantzi* attach to different parts of adult *Dendroctonus frontalis*. *T. ips* rides only under the thorax, *T. krantzi* mostly under the elytra. Over 85% of both tarsonemids carried ascospores of *Ceratocystis minor*; most individuals carried over 15 spores.

Ceratocystis minor (Hedgcock) Hunt, the bluestain fungus disease associated with the southern pine beetle, *Dendroctonus frontalis* Zimmermann, is introduced into southern pines by attacking beetles. Although the fungus can be isolated from bodies of attacking *D. frontalis*, the phoretic mites *Tarsonemus ips* Lindquist and *T. krantzi* Smiley and Moser were documented as the major sources of inoculum (Bridges and Moser, 1983). Both mite species live and develop beneath pine bark, feeding on blackish areas of the bluestain fungus that contain numerous fruiting bodies. These black areas produce many ascospores that may stick to arthropod exoskeletons. But because *D. frontalis* larvae migrate to the outer bark to pupate, the eclosing brood adults never come in contact with these sticky ascospores (Bridges and Moser, 1983). Though the *D. frontalis* pupae do not harbor phoretic mites, the brood adults emerge through the outer bark and often pick up *Tarsonemus* females that are carried to the next tree attacked (Roton, 1978). These mites may carry large numbers of ascospores in special pouches called sporothecae, located under tergite 1 on both sides of the mites (Moser, 1985).

The purpose of this study was to sample *Tarsonemus*-carrying southern pine beetle adults reared from *Pinus taeda* to determine whether the two tarsonemids ride at various locations on beetle bodies, the number of mites with and without ascospores, and how many ascospores each of the two *Tarsonemus* species carry.

MATERIALS AND METHODS

One loblolly pine (*Pinus taeda* L.) infested with *D. frontalis* was cut during each of the months of February, May, August, and December 1980. The trees were from a natural stand about 35 years old in the Catahoula Ranger District of the Kisatchie National Forest. Trees were felled when the *D. frontalis* broods were in the pupal stage in the outer bark.

Samples were taken from the bole area where the pupal stage was most con-

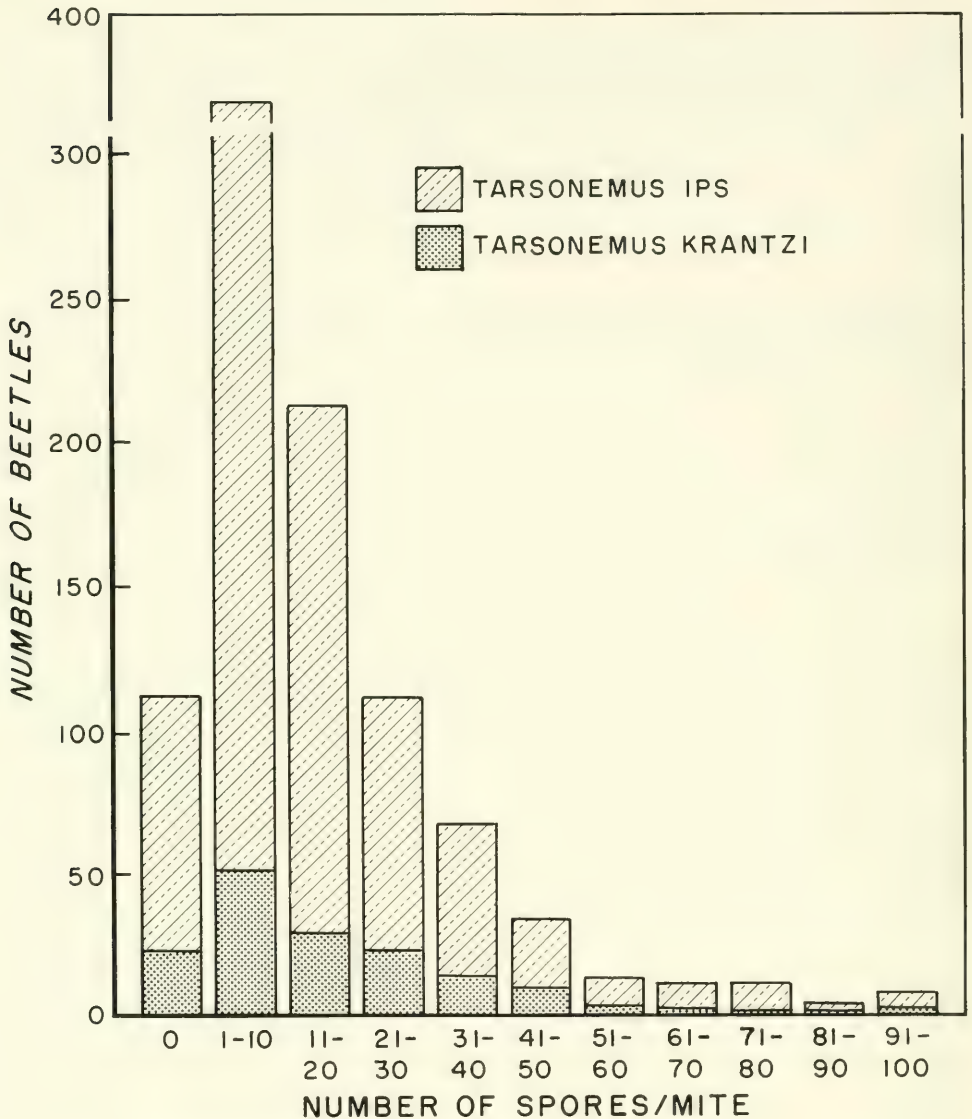


Fig. 1. Number of ascospores/mite.

centrated and where competition from other bark beetle species was least. Typically, the sample area extended 5 m through 11 m above ground level. No attempt was made to normalize infested bole heights within trees (McClelland et al., 1979) because it was not our objective to sample tree populations systematically. Five bolts were cut from each infested tree. Bolts spaced 1 m apart along the bole were trimmed so that each contained 2880 cm² of bark area. This material was placed in individual rearing cans inside the laboratory and kept at about 20°C and 50% relative humidity. The can interiors were dark with little or no air movement. Ten beetles with phoretic *Tarsonemus* mites attached to their coxae were collected from each bolt during the peak emergence period. These mites were then removed

from each beetle and temporarily mounted on slides with lactophenol as a clearing and mounting medium. Those *Tarsonemus* mites under the elytra were then removed and likewise mounted. The number of each mite species was then counted and tallied as to body location and species. *Ceratocystis minor* ascospores were counted on each mite.

Analyses of variance were performed on mites/beetle and spores/mite to detect differences due to species of mite and location on the infested tree. A split plot design was used in which tree was the blocking factor (3 df), location on the infested tree was the whole plot factor (4 df), and mite species was the split-plot factor (1 df).

RESULTS

There was no significant difference in the number of mites/beetle or spores/mite of either species of mite collected from various heights.

There were differences in the location of each species of mite on the beetles. *T. ips* was found only under the thorax, but 79.9% of *T. krantzii* were found under the elytra.

There were more *T. ips* in the samples (4.78/beetle to 0.82 for *T. krantzii*) because beetles were selected on the basis of whether mites were present on the thorax. Therefore, from this biased sample we cannot determine whether the beetles carried more *T. ips* than *T. krantzii*.

Most mites carried *C. minor* spores. Of 164 *T. krantzii* examined, 85.4% carried spores. Of 956 *T. ips* examined, 88.4% carried spores. For *T. krantzii*, 87.9% of mites on the thorax and 84.7% of mites under the elytra carried *C. minor* spores. *T. krantzii* found on the thorax carried 18.4 spores/mite; those on the elytra carried 18.1 spores/mite.

The number of spores/mite did not differ significantly between *T. krantzii* (18.2) and *T. ips* (15.5). The number of spores/mite ranged from 0–99. Although the average number of spores/mite exceeded 15, most mites carried less than 10 (Fig. 1).

DISCUSSION AND CONCLUSIONS

Because a substantial majority of both tarsonemid mites carry *C. minor* ascospores, it appears that both could infect a tree with the fungus. This confirms our earlier conclusions that phoretic mites vector *C. minor* to southern pine beetle infested trees (Bridges and Moser, 1983). Since both mite species carry equal numbers of spores, both have the potential to participate equally in the vector process. Our results show that, for the most part, the two mite species attach to different parts of the beetles.

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THE GENERIC VALIDITY OF *AENIGMOSTOMUS* AND
ASIACARDIOCHILES (HYMENOPTERA: BRACONIDAE)

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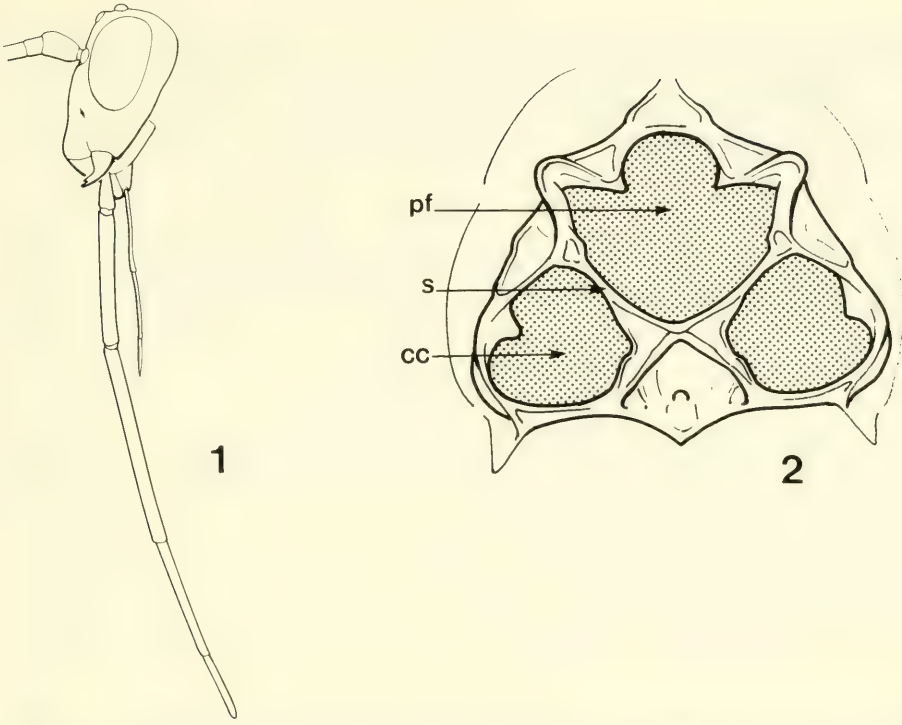
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Abstract.—The braconid genera *Aenigmostomus* and *Asiacardiachiles* are both shown to be highly apomorphic forms of the large and widespread genera *Agathis* and *Cardiachiles*. Accordingly, *Aenigmostomus* is a new junior synonym of *Agathis* and *Asiacardiachiles* a new junior synonym of *Cardiachiles*.

We wish to correct the generic placement of *Aenigmostomus longipalpus* Ashmead and *Asiacardiachiles minutus* Telenga, both of which are the basis of monotypic genera, for three reasons. First, we are preparing a paper on the comparative and functional morphology of palpal drinking tubes in the Braconidae that will include these two species. Second, Marsh et al. are currently preparing a key to the genera of the Braconidae in America north of Mexico and we wish to justify the exclusion of *Aenigmostomus* from this key. Finally, we wish to draw attention to a large widespread problem, namely monotypic groups erected for species that have very striking and aberrant features but that are otherwise typical members of larger taxa. The problem is easily recognized as an elementary one in phylogenetic analysis (Wiley, 1981, p. 83-89); nevertheless, it seems firmly embedded in generally accepted classifications. Many well known genera and families are paraphyletic because aberrant derived species are recognized at a hierarchical level equal to the parent group.

Aenigmostomus Ashmead and *Asiacardiachiles* Telenga were erected to accommodate rather odd looking species, *Aenigmostomus longipalpus* and *Asiacardiachiles minutus*. Both species differ from their nearest relatives by having very elongate mouthparts. Those of *A. longipalpus* are especially long (Fig. 1). Undoubtedly, *Aenigmostomus* and *Asiacardiachiles* were created because their authors had the opinion that the two species were so different they must represent new genera. In other words, these genera were erected to reflect great anagenetic change rather than to show cladistic or phylogenetic relationship. In this paper we try to demonstrate that the exclusion of *Aenigmostomus* from *Agathis* s.s. renders the latter genus paraphyletic. Similarly, separating *Asiacardiachiles* from *Cardiachiles* leaves *Cardiachiles* paraphyletic, unsupported by synapomorphic characters.

Agathis does not possess any synapomorphies not also shared by *Aenigmostomus* and it is doubtful that *Aenigmostomus* forms the sister group of *Agathis*. *Aenigmostomus longipalpus* and a group of *Agathis*, including *A. malvacearum* Latreille, have a narrow sclerite separating the hind coxal cavity from the pro-



Figs. 1, 2. *Aenigmostomus longipalpus*, lateral view of head. 2, *Agathis malvacearum* Latr., posterolateral view of metasoma illustrating narrow sclerite between hind coxal cavity (cc) and propodeal foramen.

podeal foramen. We hypothesize this to be a synapomorphy for a subgroup within *Agathis*. The plesiomorphic condition is that the hind coxal cavities and the propodeal foramen are contiguous. This condition is found in many species of *Agathis*, e.g. *A. rubripes* Cresson, and all species of *Earinus*, the outgroup. For a discussion of the generic limits of *Agathis*, see Sharkey (1985).

Cardiochiles and *Asiacardiochiles* are extremely similar. The only feature by which the single species of *Asiacardiochiles* differs from over a hundred species of *Cardiochiles* is the extremely large and elongate glossa, reaching to the hind coxa or beyond. The glossa is much shorter in other *Cardiochilinae*, at the longest scarcely reaching the forecoxa.

Three characters can be interpreted as synapomorphies linking *Cardiochiles* and *Asiacardiochiles* and differentiating them from the other *Cardiochiline* genera: 1. Hairy eyes; all other *Cardiochiline* genera (i.e. *Toxoneuron*, *Tenthredoides*, *Psilomiscus*, *Pseudocardiochilus*, *Hartemita* (= *Laminitarsus*), *Heteropteron* (= *Neocardiochiles*), *Wesmaelella*) have glabrous eyes and it is also the most widespread character state within the Braconidae. 2. Apical margin of clypeus with a pair of median denticles; this character state is found in *Psilomiscus* as well as *Cardiochiles* and *Asiacardiochiles*, but all other *Cardiochilinae* have a simple convex outline for the apical margin of the clypeus. The simple condition is very widespread in Ichneumonoidea and other Hymenoptera and should be interpreted

as the plesiomorphic state. 3. Hypopygium with a median longitudinal zone of desclerotization and folding; about half the genera of Cardiochilinae have the hypopygium evenly sclerotized and unfolded medially, a condition that is by far the commonest and most widespread in Hymenoptera and should thus be interpreted as plesiomorphic. Other synapomorphies, uniting all Cardiochilinae, are given by Mason (1983).

The mesopleuron of most species of *Cardiochiles* has a coarsely foveate broad groove running obliquely upward from above the midcoxa nearly to the pronotum. This groove varies greatly in depth, width, length and type of sculpture but it is an extremely widespread feature in almost all groups of Braconidae. The widespread presence of this groove strongly suggests that it is a ground plan character state of the Braconidae. In *Asiacardiochiles minutus*, *Cardiochiles eremita* Kokujev and *C. explorator* (Say) the mesopleuron is smooth and even, the oblique groove being represented by no more than the slightest flattening in the general convexity of the surface. These three species share two other character states that are unusual for *Cardiochiles*: the second tergite is without the usual longitudinal grooves that delimit a median raised area and the usually abundant tarsal pectination is reduced to one broad tooth and three small narrow teeth. Based on these character state distributions we hypothesize that the three species form a monophyletic group within *Cardiochiles*.

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**DESCRIPTIONS OF LARVAE AND BIOLOGY OF
CYRTOBAGOUS (COLEOPTERA: CURCULIONIDAE):
AGENTS FOR BIOLOGICAL CONTROL OF SALVINIA**

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Abstract. — The larvae of *Cyrtobagous singularis* Hustache and *C. salviniae* Calder and Sands are described and figured. A key to the larvae of these and to the larvae of three other erirhinine weevils, *Neochetina bruchi* Hustache, *N. eichhorniae* Warner and *Neohydronomus pulchellus* Hustache, used for biological control of water weeds, is included. Differences are reported between the biology of *C. singularis* in Zimbabwe, southern Africa and *C. salviniae* in Queensland, Australia, where the species were introduced for biological control of the aquatic weed, *Salvinia molesta* Mitchell. Their potential as biological control agents is discussed.

Some South American sub-aquatic weevils (Eirirhininae) are useful agents for biological control of aquatic weeds. One species, *Neohydronomus pulchellus* Hustache, controlled water lettuce, *Pistia stratiotes* L. in Australia (Harley et al., 1984). The genera *Neochetina* and *Cyrtobagous* contain species which controlled respectively, water hyacinth, *Eichhornia crassipes* (Mart.) Solms (Wright, 1981) and the floating fern salvinia, *Salvinia molesta* Mitchell (Room et al., 1981) when introduced into Australia for that purpose. Both genera contain species that have different potential for control of the weeds (DeLoach and Cordo, 1976; Sands and Schotz, 1985).

Cyrtobagous singularis Hustache was one of three insects introduced from Trinidad to southern Africa for biological control of salvinia (Bennett, 1975). Despite establishment of this weevil in Botswana (Procter, 1984), salvinia continued to be a serious weed, particularly in the Chobe River and neighbouring Caprivi region (Edwards and Thomas, 1977). In Australia, a closely related weevil, *C. salviniae* Calder and Sands originally from Brazil, successfully controlled salvinia in northern Queensland and Northern Territory (Room et al., 1984). Laboratory studies by Sands and Schotz (1985) have since shown differences in the feeding behaviour of the two weevil species that provide an explanation why *C. salviniae* has succeeded as a biological control agent for salvinia where *C. singularis* had failed.

In this paper we describe the larvae of the two closely related *Cyrtobagous* spp. and provide a key (May) for distinguishing them from three other environmentally important erirhinine larvae that could be present in the same waters. We report differences in larval biology of the two *Cyrtobagous* spp. in the field and discuss their potential as biological control agents for salvinia (Sands).

DESCRIPTIONS OF LARVAE

The system of nomenclature used in the descriptions is substantially that of Thomas (1957). The methods of dissection, preparation and examination of larvae are given in May (1971). Numbers of setae (referring to one side only) are shown with the modal numbers for Curculionidae in Table 1.

Abbreviations used in text and figures: Abd, abdominal segment; als, antero-lateral setae; ams, anteromedian setae; ant, antenna; at, airtubes; av, anterior ventriculus; cnp, cryptonephridium; des, dorsoepicranial setae; dlcs, dorsal lacinial setae; dpls, dorsopleural setae; fs, frontal setae; hb, hypopharyngeal bracon; les, lateral epicranial setae; lrms, labral setae; lsts, laterosternal setae; mes, median epipharyngeal setae; msts, mediosternal setae; Mpts, Malpighian tubules; oc, ocelli; pds, postdorsal setae; pls, pleural setae; plbs, postlabial setae; pms, premental sclerite; poc, postoccipital condyle; pp, pygopod; prn, pronotum; prs, prodorsal setae; prv, proventriculus; pv, posterior ventriculus; rs, retractile section; sp, spiracle; sps, spiracular setae; t, tormae; Th, thoracic segment; tr, trachea; ves, ventral epicranial setae; vlcs, ventral lacinial setae; vpls, ventropleural setae.

SUBFAMILY ERIRHININAE

Head free, usually subspherical, emarginate behind; postoccipital condyles conspicuous, acutely triangular; 2 pairs of ocelli; frontal setae reduced in number, *fs* 4 constant. Antennae broadly conical or hemispherical. Mandibles usually bifid at apex, with or without supplementary teeth. Labral tormae subparallel or convergent. Labial palpi 1- or 2-segmented. Spiracles often reduced or strongly modified; dorsal on Abd VIII. Anus terminal or ventral, 4-lobed. Alimentary canal relatively simple, lacking mycetomes and gastric caeca; 6 Malpighian tubules; cryptonephridium weak.

KEY TO LARVAE OF SOME ERIRHININAE USED FOR
BIOLOGICAL CONTROL OF WATER WEEDS

1. Abdomen with 1 pair of spiracles upstanding (Abd VII). Head bright red brown. On water hyacinth *Eichhornia crassipes*
..... *Neochetina eichhorniae* Warner, *N. bruchi* Hustache
- Abdomen with 6 pairs of spiracles upstanding on dorsum (Abd II–VII). Head not red brown 2
2. Head pale yellow, unpatterned. Spiracles of Abd II–VII upstanding laterally, well separated. Abd VIII/IX sharing a sclerotized, red-brown, dorsal plate; lacking elongate trailing hairs. Abd X lacking anal hooks. On water lettuce (*Pistia stratiotes*) *Neohydronomus pulchellus* Hustache
- Head dusky brown and cream, variegated. Spiracles of Abd II–VII upstanding on dorsum, close together. Abd VIII/IX lacking a sclerotized dorsal plate; bearing elongate, trailing hairs. Abd X bearing anal hooks. On floating ferns (*Salvinia* spp.) *Cyrtobagous* 3
3. Head with median epicranial area pallid. Abd VIII with prodorsal seta red-brown, erect; both dorsopleural setae elongate, subequal in length (Fig. 1) *C. singularis* Hustache
- Head with median epicranial area dusky brown. Abd VIII lacking a dark, erect seta; major dorsopleural seta 3 × longer than the minor one (Fig. 2) *C. salviniae* Calder and Sands

Table 1. Setal index for *Cyrtobagous* larvae and modal numbers for Curculionidae.

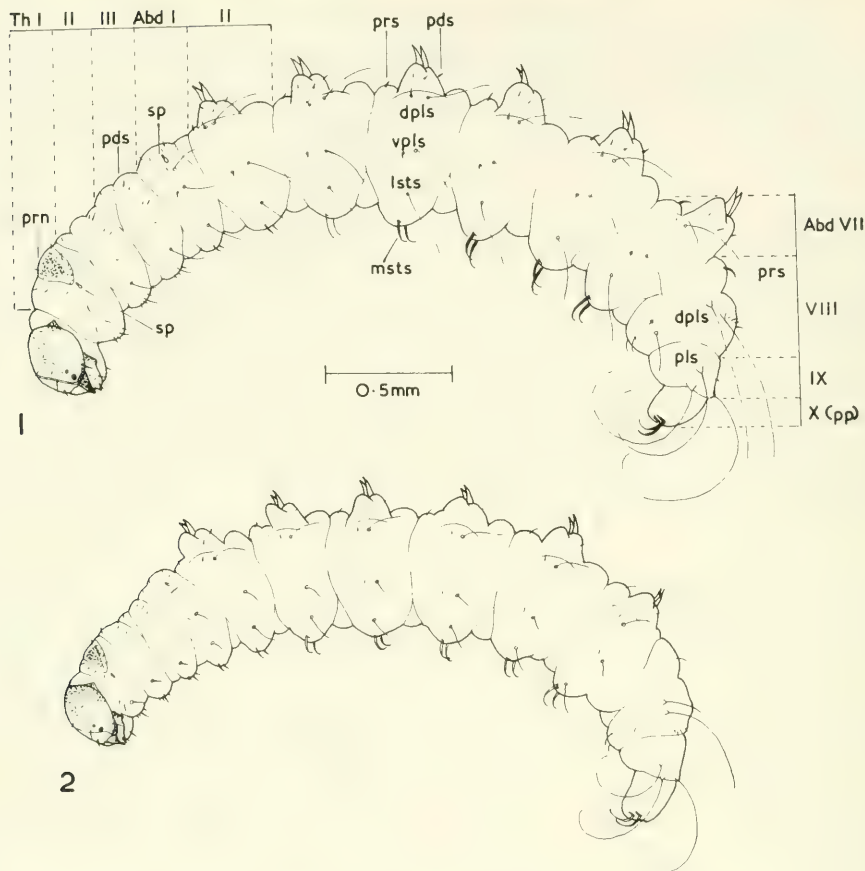
Modal Numbers			Modal Numbers		
Prothorax			Abdomen X		
Pronotal	9-10	v	Anal	2	v
Dorsopleural	1	v	Head		
Ventropleural	2	2	Dorsal	4	5
Mediosternal	1	1	Posterior	4*	4*
Pedal area	4	v	Lateral	2	2
Meso-, Metathorax			Ventral	2	2
Prodorsal	1	1	Frontal	2	5
Postdorsal	3	4	Clypeal	2*	2
Dorsolateral	2	v	Labral	3	3
Alar area	1 + 1*	v	Mandibular	2*	2
Dorsopleural	1	1	Epipharyngeal Lining		
Ventropleural	1	1	Anterolateral	3	3
Mediosternal	1	1	Anteromedian	1	2
Pedal area	4	v	Median	3	2
Abdomen I-VIII			Maxilla		
Prodorsal I-VII	1	1	Dorsal	7	v
VIII	1	v	Lacinia		
Postdorsal	5	5	Ventral	4	v
VII	5	5	Palpal	0	1*
VIII	4	v	Stipital	1	1
Spiracular	?	2	Palpiferal	2	2
VII	?	1	Labium		
VIII	0	1	Postlabial	3	3
Dorsopleural	2	2	Prelabial	1	1
Ventropleural	2	2	Ligular	1	2
Laterosternal	1	1			
Mediosternal	2	2			
Abdomen IX					
Dorsal	3	v			
Pleural	2	2			
Sternal	2	2			

* minute setae; v, variable.

Genus *Cyrtobagous* Hustache

Cyrtobagous Hustache, 1929. Type species, *Cyrtobagous singularis* Hustache. Orig. desig.

Larva.—Body slender, gently curved and tapered to a pygopod; spiracles up-standing on dorsum. Setae variously modified as hooks and trailing hairs. Head free, subspherical, emarginate behind; endocarinal line absent; sutures distinct, ecdysial line dark, half length of coronal suture; *des* 3 placed within frons, *des* 4 absent; *fs* 4 and *fs* 5 subequal, *fs* 1, 2, 3, absent. Ocelli distinct, close together. Antennae mushroom-shaped on basal cone which bears 1 sensory papilla. Mandibles apically bifid with inner margin of incisor lobe crenate. Hypopharyngeal bracon clear. Labrum gently rounded or truncate; tormae slender, subparallel. Labial palpi 1-segmented; premental sclerite broken before middle. Maxilla with lacinia (mala) acute, almost as long as palpus. Spiracles of Abd II-VII external,



Figs. 1, 2. *Cyrtobagous* larvae, lateral view. 1, *C. singluaris*. 2, *C. salviniae*.

acute, set on a median ampulla, close together, erect, retractile; those of mesothorax, Abd I and Abd VIII minute, vestigial. Abdominal II–VII *pds*-*sps* set around ampulla; *lst*s slender, elongate, outstanding horizontally (perhaps to function as balancers in the water); some setae of Abd VII and IX trailing, much longer than *lst*s; *msts* of Abd III–VII relatively short, strong, curved backwards; basal socket extended caudad. Anal segment produced to form a tubular pygopod terminated by 4 strong, ventrally braced hooks, curved forwards. Alimentary canal with proventriculus simple, slender; anterior ventriculus elongate, rugose; posterior section 1-coiled. Malpighian tubules evenly distributed around ileocolic valve, 2 pairs looped cephalad against ventriculus, 1 pair intertwined caudad with hind gut. Cryptonephridium symmetrical. Rectal bracon not visible.

Note on spiracles.—The construction of the spiracles in *Cyrtobagous* is of a type similar to that of *Neochetina bruchi* and of the rice water weevil *Lissorhoptrus oryzophilus* Kuschel. The apical section is formed by the fused airtubes which are completely sclerotized and tapered to a fine point. It contains no internal structures other than a channel formed by the infolded walls. Below the airtubes, a retractile, concertina-like tube, of similar length, situated within the raised ampullae, leads into a branch of the trachea. The spiracle of *L. oryzophilus* as described by Isely

and Schwardt (1930) differs in detail. The basal part of the external "hook" is formed of heavy, infolded rings and there is no obvious retractile section. In addition, there is a minute blade-like process at the extreme tip, noted by May (1970) which is absent in *Cyrtobagous*.

***Cyrtobagous singularis* Hustache**

Figs. 1, 3–13

Cyrtobagous singularis Hustache, 1929: 228.

Larva.—Maximum size 4.2×1.6 mm. Head width: 1st instar, 0.18 mm; 2nd instar, 0.24 mm; 3rd instar, 0.33 mm. Setal index as in Table 1. Pleural and most dorsal setae fine, pallid, ranging in length from minute to extremely long; prodorsal setae of Abd IV–VIII progressively more hook-like, that of Abd VII conspicuous, red-brown; ventral setae of Abd III–VII and Abd X strongly hooked and pigmented. Head pallid except for a parietal stripe, genae and ventral areas dusky. Labrum gently rounded. Mandibles dusky with darker tips. Pronotum dusky. Abd II–VII with major *dpls* and *vpls* approximately $10\times$ longer than the minor seta. Abd VIII with *dpls* subequal in length, elongate, $3\times$ longer than other major *dpls*. Abd IX with 1 dorsal, 2 pleural setae extremely elongate, strongly curved. Anal hooks (Abd X) with conspicuous basal extensions.

Material examined.—TRINIDAD: Curepe, Oct. 1983 (F. D. Bennett). 6 larvae ex laboratory stock on *Salvinia molesta*, Brisbane, Sept. 1984 (D. P. A. Sands).

***Cyrtobagous salviniae* Calder and Sands**

Figs. 2, 14–15

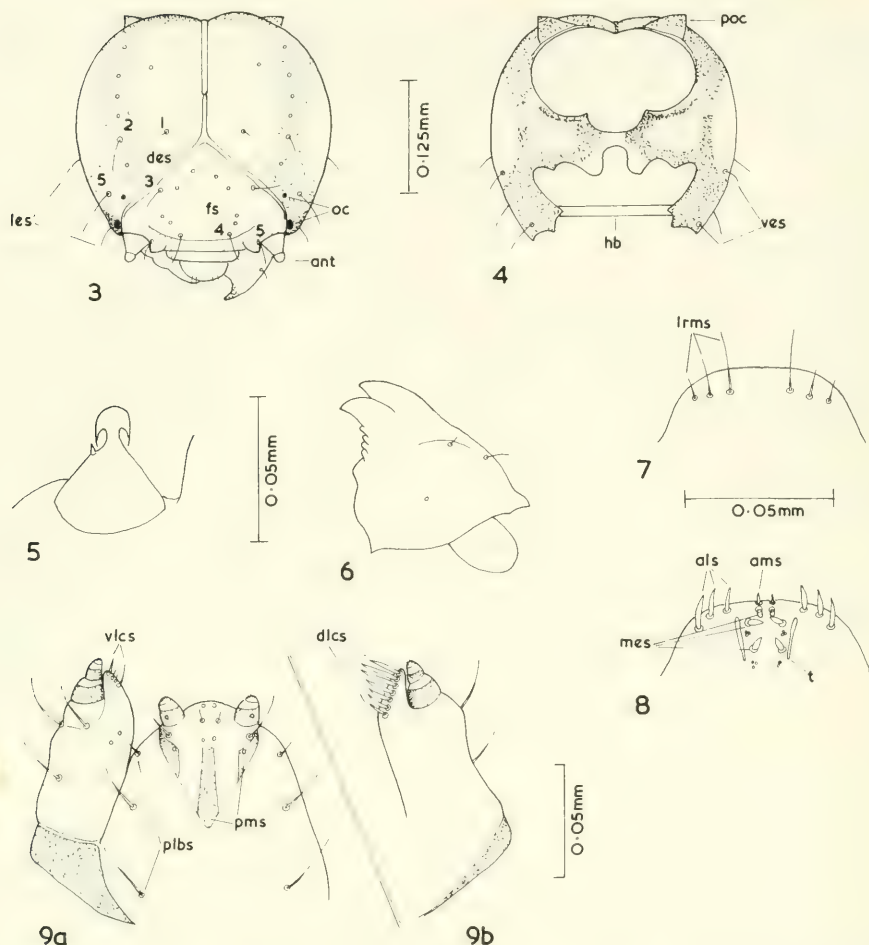
Cyrtobagous salviniae Calder and Sands 1985: 57–64.

Larva.—Maximum size 4.0×1.0 mm. Head width: 1st instar, 0.18 mm; 2nd instar, 0.22 mm; 3rd instar, 0.27 mm. Setal index as in Table 1. Fine setae pallid, generally less elongate than in *C. singularis*. Hooked setae pale brown; *prs* of Abd VII not outstanding. Head pallid only on frons and a small lateral parietal area, elsewhere dusky brown. Labrum truncate. Tormae contiguous at base. Mandibles reddish. Pronotum dusky brown. Abd II–VII with major *dpls* $3\times$ longer than the minor seta; major *vpls* $2.5\times$ longer than minor seta. Abd VIII with *dpls* unequal in length; major seta elongate, $3\times$ length of minor seta. Abd IX with 1 dorsal, 2 pleural setae extremely elongate and curved as in *C. singularis*.

Material examined.—BRAZIL: Joinville, 1978 (I. W. Forno). 6 larvae ex laboratory stock on *Salvinia molesta*, Brisbane, Sept. 1984 (D. P. A. Sands).

BIOLOGY

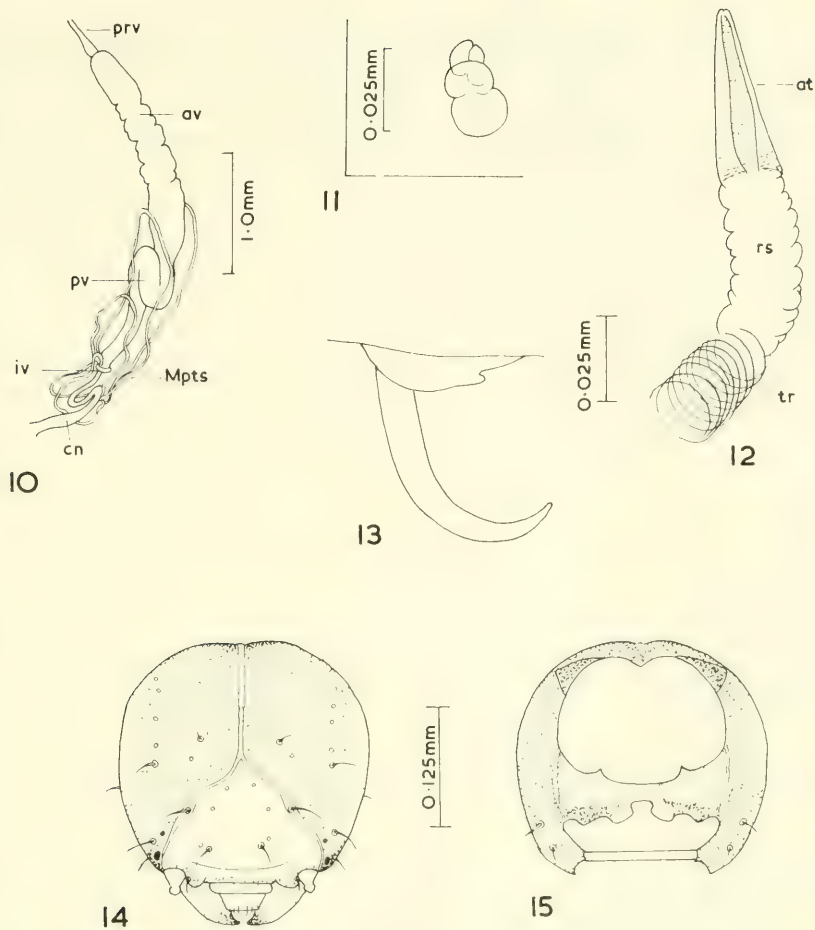
Estimates were made of the abundance of *C. singularis* and of plant damage at a number of sites on the Zambezi River, Zimbabwe, between Kazungula and Lake Kariba, and for *C. salviniae* in Queensland (Qd) and Northern Territory (NT), Australia. Three samples of salvinia mat were collected from each locality with a scoop net (30×30 cm with 2 m handle) and transported in plastic bags for microscopic examination. Adults and larvae per m^2 were counted. The numbers of buds damaged and rhizomes tunnelled per m^2 were recorded. When larvae were located by examining terminal growth, their positions on or in the plant, and any damage distinguishable from adult feeding, were then recorded.



Figs. 3–9. *Cyrtobagous singularis* larva. 3, Head, dorsal view. 4, Head, ventral view. 5, Antenna. 6, Mandible. 7, Labrum. 8, Epipharyngeal lining. 9, Maxilla and labium (a, ventral view; b, maxilla, dorsal view).

In Australia, larvae of *C. salviniae* were all located tunnelling in the rhizomes of the host plant, salvinia, whereas in Zimbabwe, only one larva of *C. singularis* was found that had partly entered the petiole of a leaf. All others were found externally between the apical, unopened pair of leaves.

No significant difference was found between the numbers of buds and terminal leaves attacked by larvae of each species (*C. salviniae*: $1.67 [\pm 0.23 \text{ SE}, n = 30]$; *C. singularis*: $1.35 [\pm 0.15 \text{ SE}, n = 17]$ per larva) but the type of damage differed for each species. Advanced larvae of *C. singularis* produced longitudinal “mines” in the expanding buds whereas first-instar *C. salviniae* destroyed young buds before the older larvae tunneled into the rhizome. Quantitative differences in damage by the two species to rhizomes and root petioles were pronounced. There was no tunnelling in nodes, internodes or root petioles by *C. singularis* larvae, but each larva of *C. salviniae* tunneled, $0.67 (\pm 0.13 \text{ SE})$ nodes, $0.93 (\pm 0.12 \text{ SE})$ internodes and $0.53 (\pm 0.13 \text{ SE})$ root petioles. External scars were associated with $0.41 (\pm 0.12$



Figs. 10–15. *Cyrtobagous* larvae. 10–13, *C. singularis*. 10, Alimentary canal. 11, Thoracic spiracle, showing alignment. 12, Abd VII spiracle. 13, Anal hook. 14–15, *C. salviniae*. 14, Head, dorsal view. 15, Head, ventral view.

SE) of *C. singularis* larvae but none were associated with the internal-feeding larvae of *C. salviniae*.

The abundance of *C. singularis* in Zimbabwe differed considerably from that of *C. salviniae* in Australia (Table 2). Only at Msuna were adults of *C. singularis* abundant, with 24 adults per m². By contrast, at Wappa Dam, Queensland, 105 adults per m² of *C. salviniae* were recorded even before the salvinia mat had begun to collapse.

DISCUSSION

Differences in the biology of two *Neochetina* species were noted by DeLoach and Cordo (1976), but whereas these have not as yet been shown to relate to their potential as biological control agents of water hyacinth, the differences in feeding behavior of *Cyrtobagous* studied in the laboratory (Sands and Schotz, 1985) were clearly related to the different impact made by each species on salvinia. Under

Table 2. Population densities of *Cyrtobagous* and damage to salvinia in Zimbabwe and Australia.

Locality	Altitude (m)	Date	Water Temperature (°C)†	Nos./m²		% <i>S. molesta</i> Damaged*	
				Adults	Larvae	Buds	Rhizomes
<i>C. singularis</i> in Zimbabwe							
Kazungula (17°45'S, 25°20'E)	1060	11.x.84	27.0	3	9	<1	0
Victoria Falls (17°56'S, 25°50'E)	990	5.x.84	26.5	<1	<1	4	0
Msuna (18°01'S, 26°54'E)	630	13.x.84	31.5	24	<1	26	0
Lake Kariba (16°32'S, 28°52'E)	604	16.x.84	31.0	3	<1	5	0
<i>C. salviniae</i> in Australia							
Mt. Malloy, Qd (17°22', 145°15'E)	335	16.iv.84	24.0	66	27	52	72
Kaban, Qd (17°33', 145°24'E)	900	18.iv.84	22.0	27	21	34	3
Wappa Dam, Qd (26°35'S, 152°49'E)	44	22.i.85	26.5	105	69	90	18
Howard River, NT (12°29'S, 131°06'E)	20	22.vii.83	28.5	43	41	81	29

† At 2 cm depth.

* Buds damaged by adults and larvae, rhizomes tunnelled by larvae.

field conditions, observations on larvae of *C. singularis* in Zimbabwe and on *C. salviniae* in Australia confirm that they each feed on separate parts of the plant.

The larvae of the two *Cyrtobagous* are easily distinguished by their morphology. It is possible that the longer setae of *C. singularis* are an adaptation to external feeding, where they aid movement from one submerged part of the host to another, in contrast to the shorter setae of *C. salviniae* whose larvae tunnel internally within the rhizomes.

Until recently (Procter, 1984), the establishment of *C. singularis* on salvinia in the Chobe and Zambezi Rivers had not been confirmed. During the present study, *C. singularis* was collected in small numbers at several localities visited between Ngoma, Botswana and Lake Kariba, Zimbabwe, but was not taken at Chirundu or Mana Pools, downstream from Lake Kariba. It is possible that this weevil had been overlooked on Lake Kariba following its establishment from the releases made in 1971 (Bennett, 1975) or on the Chobe and Linyanti Rivers from 1972–1974 (Edwards and Thomas, 1977). Several other factors appear to relate to a decrease in abundance of salvinia on Lake Kariba which may not be entirely due to insect damage (Marshall and Junor, 1981).

C. singularis was much less abundant at all places visited in southern Africa when compared with *C. salviniae* at certain localities in Australia. The maximum of 24 adult *C. singularis* per m² recorded at Msuna (Table 2) may have resulted from concentration of weevil numbers at a site where water had receded in a narrow lagoon entering the Zambezi River. No seasonal increase in numbers has

been observed in Botswana (D. Procter, pers. comm.). Much higher numbers of *C. salviniae* have been reported at several localities in Australia where biological control of salvinia has been achieved (Room et al., 1984).

Salvinia has remained a serious weed upstream in the eastern Caprivi Strip (Toerien et al., 1984) where *C. singularis* has not controlled the weed. Recently, *C. salviniae* was released at sites in the eastern Caprivi Strip (Schlettwein and Hamman, 1984). During the present study, adults of both species were recovered at Ngoma, Botswana, in October 1984, where the damage by *C. salviniae* appeared to be similar to that recorded in Australia. At Ngoma differences in feeding characteristics of the two species were observed within 300 m of each other.

It appears that both the nature of damage caused by feeding and their relative abundance on *S. molesta* show differences between the two *Cyrtobagous* and that these factors contribute to the success of *C. salviniae* as a biological control agent where *C. singularis* has failed. The spread of *C. salviniae* over areas where *C. singularis* has already established in southern Africa might be expected to result in effective control of salvinia.

ACKNOWLEDGMENTS

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DESCRIPTION OF AN *ANAGARICOPHILUS*
(COLEOPTERA: ENDOMYCHIDAE)
LARVA FROM MADAGASCAR

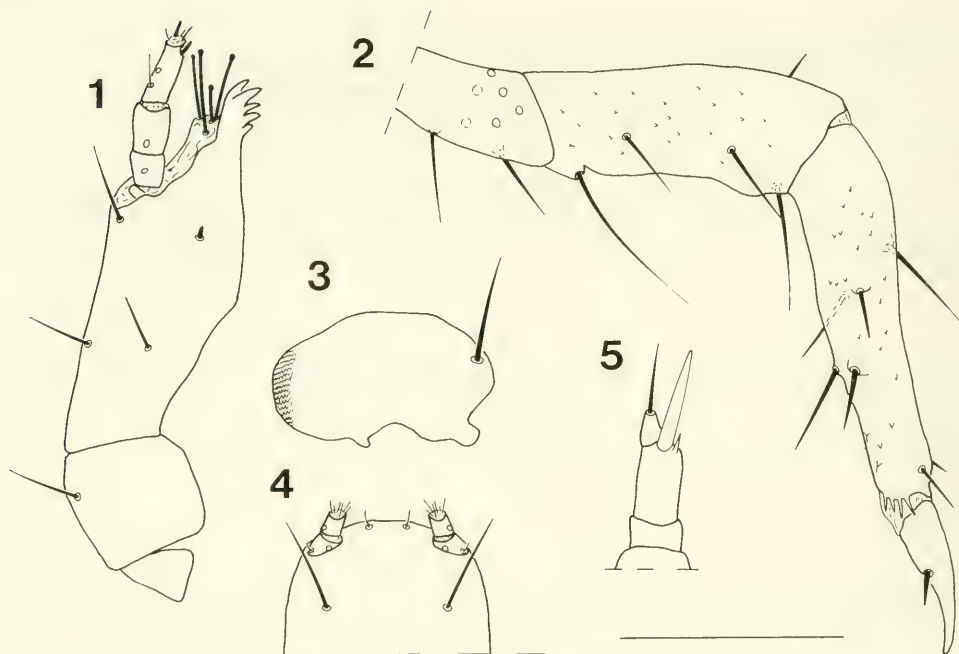
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Abstract.—The larva of an undetermined species from Madagascar of the endomychid genus *Anagaricophilus* is described and illustrated. Adults and associated larvae were collected from a compost pile. This larva is compared with other described mychothenine larvae.

Arrow (1922) described the genus *Anagaricophilus* based on a single species, *A. pulchellus* Arrow, from the Seychelles. Subsequent workers (Strohecker, 1974, 1979; Vinson, 1950) described additional species of this genus which presently contains ten species from Madagascar, Mauritius, and the Seychelles. These workers placed *Anagaricophilus* in the subfamily Mycetæinae, along with a variety of other forms, based on its small size and reduced tarsal formula. Sasaji (1978) separated *Anagaricophilus* and placed it in a new subfamily, the Mychotheninae, based on the anterior arms of the tentorium not being fused and by the laterally closed mesocoxal cavities. In addition to *Anagaricophilus*, this subfamily includes *Baeochelys*, *Bryodryas*, *Bystodes*, *Bystus*, *Clemmus*, *Dexialia*, *Dialexia*, *Exysa*, *Idiophyes*, *Malagaricophilus*, *Mychothenus*, and *Symbiotes*.

Little is known about the habitat of mychothenine Endomychidae. Species from many genera have been taken from forest debris, and the gut of the *Anagaricophilus* larva described below was filled with unidentifiable spores of Fungi Imperfecti. Published references to mychothenine larvae are scarce: *Bystus ulkei* (Crotch) is figured by Böving and Craighead (1931), *Bystus* sp. is figured by Lawrence (in press), and *Mychothenus asiaticus* Sasaji is figured and described in detail (Sasaji, 1978). Mychothenine larvae are distinguished from other endomychid larvae by the following characters: body without tergal plates and with simple setae only; reduced, transverse mandible without incisor lobe and with tubercles arranged in distinct rows on mola; maxillary mala falciform; head without frontal sutures or stemmata. The absence of paired spatulate setae on the tibiae and a relatively long third antennal segment separates *Anagaricophilus* from *Mychothenus*. *Anagaricophilus* is similar to the illustrations of *Bystus* except for the relative lengths of the antennal segments. In *Bystus* segments 1 and 3 are subequal in length and segment 2 is about three times longer than 1 and 3 combined. *Anagaricophilus* differs from both genera, however, by the presence of capitate setae on the maxillary mala. I reject Sasaji's (1978) interpretation of the maxilla; he refers to a separate galea and lacinia, but I prefer to interpret the falciform process as a modification of the mesal margin of the mala.



Figs. 1-5. *Anagaricophilus* sp., larva. 1, Maxilla. 2, Front leg. 3, Mandible. 4, Labium, distal portion. 5, Antenna. Scale line = 0.1 mm.

Seven larvae of an undetermined species of *Anagaricophilus* were taken with about 100 associated adults with the following collecting data: Madagascar, Tananarive Prov., Antananarivo, Parc de Tsimbazaza, 25 October 1984, in compost pile, Robert W. Brooks. Adults and larvae of this species are deposited in the Snow Entomological Museum (University of Kansas).

Description of Late-Instar Larva of
Anagaricophilus sp.

Figs. 1-5

Length about 1.8 mm; body oblong, flattened. Dorsum and venter lightly pigmented, with simple setae. Head large, about $1.6 \times$ wider than long; lateral margins strongly convergent posteriorly and toward labrum. Stemmata absent. Frontal sutures absent, fronto-clypeal suture present. Antenna (Fig. 5) 3-segmented; segment 2 longest. Ventral sensory appendage elongate, subequal in length to segment 3 and its terminal seta. Labrum transverse, about $2.0 \times$ wider than long. Mandible (Fig. 3) transverse, incisor lobe absent; mola well-sclerotized, with distinct rows of tubercles. Maxilla (Fig. 1) with juxtacardo triangular, cardo subquadrate, stipes elongate; mala falciform, with long capitate setae. Palpifer small; palp 3-segmented. Labium (Fig. 4) undivided, palps 2-segmented. Prothorax narrower than mesothorax, about $2.0 \times$ wider than long. Mesothorax and metathorax subequal in length, combined length only slightly longer than prothorax; metathorax as wide as prothorax. Legs (Fig. 2) 5-segmented. Trochanter large, elongate. Femur subcylindrical. Tibia long, narrow, about $1.4 \times$ longer than femur. Tarsungulus

unisetose. Abdominal terga 1–8 with dorsal annular spiracles. Segment 1 widest and longest. Segments 2–9 shorter and narrower than the preceding segment. Segment 10 reduced, ventrally positioned.

ACKNOWLEDGMENTS

I am indebted to Robert W. Brooks for his efforts in collecting these and many other small Malagasy beetles. His collecting was supported by a grant from the National Geographic Society (to Charles D. Michener) to study the bees of Madagascar. I thank H. F. Strohecker for his assistance in identifying these beetles and George W. Byers and John F. Lawrence for their comments on this paper.

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HOST SELECTION IN XYLOPHILIC CECIDOMYIIDAE (DIPTERA): VESSEL SIZE AND STRUCTURE

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Abstract.—Larvae of xylophilic Cecidomyiidae develop only in woody angiosperms with vessels of 75 μ or greater diameter. Because vessel diameter varies with trunk or branch diameter, mature parts of some species of hardwoods may offer suitable niches for larval development while smaller branches or twigs may not. Vessel diameters of the herbaceous angiosperms tested were less than 75 μ and gymnosperms lack vessels; hence neither are hosts.

Xylophilic Cecidomyiidae are an unusual guild of gall midges that use freshly exposed xylem vessels of hardwoods as a larval niche. The biology of two European species was described in detail by Kieffer (1900). We reported on the biology of several nearctic species that live in the vessels of hardwoods in Ohio (Rock and Jackson, 1985). All known species have similar multivoltine life cycles. Females oviposit in sapwood vessels of freshly cut hardwoods where larval development is completed in approximately two weeks. Mature larvae emerge from the vessels when rainfall is sufficient to soak the wood. Pupation occurs in soil and summer generations of adults emerge 10–16 days later.

Host plant suitability probably depends on several factors including: olfactory attraction to exposed wood, suitable vessel diameter for oviposition, vessel diameter adequate for larval development, and available nutrients. This paper examines the significance of vessel diameter on host tree suitability. Data is reported for the following species: *Xylodiplosis longistylus* Gagné; *Trogodiplosis flexuosa* Gagné; *Ledomyia emilyae* Gagné; *Ledomyia mira* Gagné; and *Ledomyia parva* Gagné. Unless otherwise indicated, *X. longistylus* was used for laboratory studies because of its ready availability.

METHODS AND MATERIALS

We have previously described methods for collecting and rearing the adults and larvae (Rock and Jackson, 1985). Freshly cut samples of 17 species of hardwoods and one species of softwood were collected for this study and placed at field sites where natural populations of the midges occurred (Table 1). Stems from some of the herbaceous angiosperms found at or near the field sites were also examined (Table 1).

Quercus and *Fraxinus* have been described as suitable hosts (Kieffer, 1900, 1904; Huggert, 1980; Rock and Jackson, 1985) and we initially used them as

Table 1. Hardwood and herbaceous angiosperms and gymnosperms tested.

	Diameter of Largest Sample (cm)*	Larvae Collected	Maximum Vessel Diameter (μ) in Logs 8 cm d.**
Angiosperms			
<i>Acer saccharinum</i> Marsh	35	—	50
<i>Betula papyrifera</i> Marsh	9	—	50
<i>Carpinus caroliniana</i> Walt.	9	+	75
<i>Carya ovata</i> (Mill.) K. Koch	26	+	250
<i>Crataegus</i> sp.	8	—	35
<i>Fraxinus americana</i>	25	+	200
<i>Juglans nigra</i> L.	25	+	250
<i>Malus</i> sp.	16	—	50
<i>Morus nigra</i> L.	25	+	240
<i>Populus deltoides</i> Bartr.	12	+	75
<i>Prunus serotina</i> Ehrh.	31	—	62
<i>Prunus</i> sp.	25	—	50
<i>Quercus alba</i> L.	31	+	250
<i>Robinia pseudoacacia</i> L.	21	—	250
<i>Salix babylonica</i> Marsh	9	+	75
<i>Sassafras albidum</i> (Nutt.) Nees	8	+	200
<i>Ulmus americana</i> L.	20	+	175
<i>Zea mays</i> L.	3	—	50
<i>Helianthus annuus</i> L.	2	—	50
<i>Helianthus tuberosus</i> L.	2	—	50
<i>Cirsium arvense</i> (L.) Scop.	1	—	50
Gymnosperms			
<i>Pinus strobus</i> L.	19	—	Vessels absent

* All samples 25–30 cm long.
** Stem diameter smaller in herbaceous angiosperms.

controls. The suitability of a sample of a wood for larval development was determined by exposing the wood for oviposition for a minimum of three weeks, then placing the sample in a bin of water and recording larval emergence. Larval emergence indicated a suitable host.

Vessel diameter in hardwoods decreases as branch diameter decreases (Zimmerman and Brown, 1971). Wood samples of varying diameter were cut from known host species and left at the field sites to determine which parts of the tree contained vessels suitable for larval development. Branches were selected with diameters gradually increasing from 3 mm to 50 mm. The exposed vessels at the base of leaf petioles and at fresh leaf scars were tested in the same manner. Similar samples were offered to caged females in the laboratory. Vessel diameters were measured with the aid of a stereomicroscope and an ocular micrometer.

RESULTS AND DISCUSSION

In all wood samples tested, measured vessel diameters corresponded with the ranges reported by Panshin and Zeeuw (1970). Table 1 lists species of study plants from which larvae were or were not collected. Table 2 lists the species of xylophilic cecidomyiids associated with each host wood. All samples of host species contained some vessels with a diameter of at least 75 μ. The species of

Table 2. Host specificity of xylophilic Cecidomyiidae.

Host	<i>Xylodiplosis longistylus</i>	<i>Trogodiplosis flexuosa</i>	<i>Ledomyia mira</i>	<i>Ledomyia parva</i>	<i>Ledomyia emilyae</i>	<i>Ledomyia</i> sp. (not further identified)
<i>Carpinus caroliniana</i>	+	0*	0	0	0	0
<i>Carya ovata</i>	+	0	0	+	0	+
<i>Fraxinus americana</i>	+	+	0	0	0	+
<i>Juglans nigra</i>	+	+	0	0	0	+
<i>Morus nigra</i>	+	0	0	0	0	0
<i>Populus deltoides</i>	+	+	0	0	0	0
<i>Quercus alba</i>	+	+	+	+	+	+
<i>Salix babylonica</i>	+	0	0	0	0	0
<i>Sassafras albidum</i>	+	+	0	0	0	0
<i>Ulmus americana</i>	+	+	0	0	0	+

* 0 = not tested on this plant.

plants from which no larvae were collected are presumably unsuitable as hosts. With the exception of *Robinia pseudoacacia*, the largest available vessels in non-host species were 62 μ d., with most species having a maximum vessel d. of 50 μ or less.

Although we have limited data from field observations, it appears that non-host species probably do not attract females or do not trigger oviposition. No females were observed visiting field samples of non-host plants, nor were females from caged populations of *Trogodiplosis* and *Xylodiplosis* attracted to *Robinia* or *Crataegus* samples. Caged females of *Ledomyia* sp. and *Xylodiplosis* were observed feeding in the sapwood areas of *Prunus serotina* and *Malus* sp. without attempting to oviposit. However, it is possible that some of the hardwoods that appear to be unsuitable for larval development may attract female gall midges and trigger oviposition, but a vessel large enough to allow ovipositor insertion may not be adequate for completion of larval development. Nevertheless, our data indicate that a vessel of at least 75 μ d. is needed for larval development and that vessel diameter is significant in determining host suitability.

Table 1 lists the herbaceous angiosperms we tested as potential hosts. The vessels of all these species were less than 50 μ d. Female gall midges were never observed attempting to oviposit on the broken stems nor were larvae ever collected from the samples. Gymnosperms lack vessels and do not provide a suitable larval habitat: no larvae were collected from field site samples of *Pinus strobus* L. These data suggest that the host plants of xylophilic gall midges are confined to some of the hardwood angiosperms.

Although the foregoing discussion of hardwood vessels and host suitability has referred to branches of substantial diameter (see Table 2) some small twigs and branches are also used by the gall midges. Vessels are elongated cones. Therefore, in a given species of tree vessels in old wood may be of suitable diameter, while those in new twigs are not. In most host tree species, twigs of 6 mm d. have some vessels 75 μ d. or greater and are suitable for larval development (Table 3). Vessels in narrower twigs, in leaf petioles, and in leaf scars are usually too small for oviposition. Observations of caged females have shown that vessels of approximately 25 μ are too small to allow ovipositor insertion. However, females are

Table 3. Maximum vessel diameter in small branches and leaf scars of some hardwood hosts.

Host	Branch Diameter (mm)	Maximum Vessel Diameter: Branch (μ)	Maximum Vessel Diameter: Scars (μ)
<i>Carya</i>	5.5	75	<25
	6.5	87	<25
<i>Carpinus</i>	4.5	25	<25
	7	25	<25
<i>Fraxinus</i>	5	75	<25
	6.5	75	<25
<i>Juglans</i>	5	62	<25
	6	75	<25
<i>Quercus</i>	5	62	<25
	6	75	<25
<i>Salix</i>	20	50	<25
<i>Sassafras</i>	5	62	<25
	6	75	<25

attracted to leaf scars of a host twig for a few days after the leaves are removed. This may aid in attracting females into the vicinity of a host tree and enhance the possibility of encountering a broken branch.

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**A NEW NEOTROPICAL SPECIES OF *ANTHONOMUS*
(COLEOPTERA: CURCULIONIDAE) ASSOCIATED WITH
BOMBACOPSIS QUINATA (BOMBACACEAE)**

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Abstract.—Larvae, pupae, and adults of *Anthonomus santarosae* Clark, a new species of Anthonominae from Costa Rica, Panama, and Venezuela, are described and illustrated. Larvae develop in aborted flower buds of *Bombacopsis quinata* (Jacq.) Dugand in Costa Rica. Characters of all three stages are compared with those of *A. grandis* Boheman, species in the *Anthonomus* subgenus *Anthonomorphus* Dietz, and anthonomines of the genera *Loncophorus* Chevrolat and *Atractomerus* Duponchel and Chevrolat.

The new anthonomine weevil described here is represented by adults, larvae and pupae from Costa Rica, and by adults from Panama and Venezuela. The specimens from Costa Rica were reared or extracted from aborted flower buds of *Bombacopsis quinata* (Jacq.) Dugand, a common tree in the Santa Rosa National Park in Guanacaste Province, Costa Rica (Janzen, 1983). The species is described now to make a name available for ecological studies being conducted by Dr. Janzen. It is of particular interest because it is among those Anthonominae currently being examined in an attempt to elucidate the phylogenetic relationships of the boll weevil, *Anthonomus grandis* Boheman. Adults, larvae, and pupae are described and compared with the corresponding stages of *A. grandis* and related anthonomines.

***Anthonomus santarosae* Clark, NEW SPECIES**

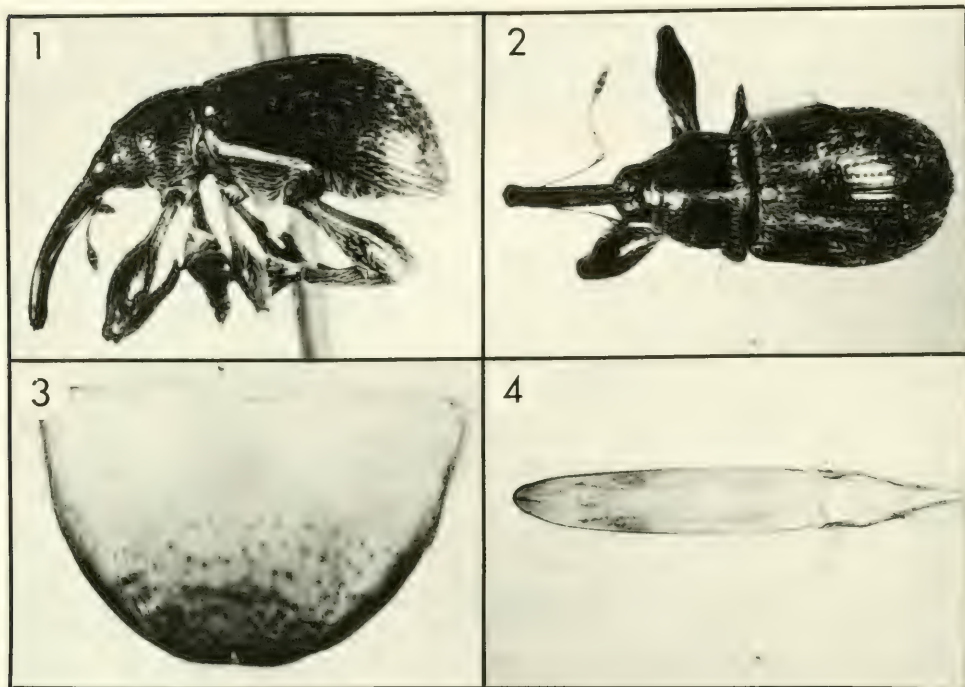
Holotype.—♂, COSTA RICA, labelled [83-SRNP.37], and [Santa Rosa National Park/Guanacaste Province/Costa Rica, D. H. Janzen]; deposited in the United States National Museum of Natural History, Washington, D.C.

Paratypes.—3 ♂, 7 ♀, with same label data as holotype; 84 ♂, 149 ♀, labelled [COSTA RICA: Guana./Santa Rosa Nat. Park/13-14 February 1984/D. H. Janzen, 300 m], and [reared from aborted/fallen flower buds/*Bombacopsis quinatum*/em. 20-29 Feb. 1984]; 1 ♂ [CANAL ZONE, Barro/Colorado Is., UV/trap 1 (3 m high)/21 Mar 1977 H. Wolda]; 2 ♂ [CANAL ZONE, Barro/Colorado Is., UV/trap 3 (26 m high)/(28 Dec 1978, 6 Mar 1979) H. Wolda]; 5 ♂, 4 ♀ [PANAMA, Pan.,/Las Cumbres,/H. Wolda, malaise/trap, January 1982]; 1 ♂, 1 ♀, labelled [Venezuela-Bari-/nas. Reserva Fo-/restal-Ticopero./280 m 3-10-IV-66], [F. Fernandez Y./Luis J. Joly.], and [Venezuela-Inst./Zool. Agrícola/Fac. Agronomía/Univ. Cen-

tral]. Total paratypes, 257; deposited in the collections of the National Museum of Natural History, Washington, D.C.; Auburn University, Auburn, Ala.; Texas A&M University, College Station, Tex.; La Universidad Central de Venezuela, Maracay; and in the collection of C. W. O'Brien, Florida A&M University, Tallahassee, Fla.

Larvae and pupae.—Eight 3rd instar larvae removed from flower buds of *Bombacopsis quinata* gathered Feb. 1, 1984, in Santa Rosa National Park, Guanacaste Province, Costa Rica, by D. H. Janzen; eight pupae extracted from flower buds of *Bombacopsis quinata* gathered Feb. 1, 1984, in Santa Rosa National Park, Guanacaste Province, Costa Rica, by D. H. Janzen; identified by association with adults in buds; deposited in the Insect Collection, Department of Entomology, Texas A&M University. Larvae and pupae are not considered to be paratypes.

Adult male (Figs. 1–4).—*Length*: 3.9–4.9 ($m = 4.6$, $n = 15$) mm. *Width*: 1.7–2.0 ($m = 1.98$, $n = 15$) mm. *Head*: Vertex sparsely, minutely punctate; each puncture with a narrow, whitish, setiform scale; venter with slightly broader, non-imbricated white scales; eyes round, evenly convex, separated by distance ca. equal to $0.5 \times$ width of rostrum at base. *Rostrum*: Length 1.6–1.8 ($m = 1.64$, $n = 15$) $\times$ pronotal length; evenly curved from base to apex; in dorsal view, sides subparallel to antennal insertions, slightly constricted between there and apex; portion distal to antennal insertions 28–34 ($m = 31$, $r = 15$) % of total rostral length; proximal portion carinate, with shallow dorsolateral sulcus and deeper, punctate, lateral sulcus; with sparse, setiform white scales; antennal funiculus 7-articulate, article 1 about as long as articles 2–6 combined. *Prothorax*: In dorsal view (Fig. 2), sides rounded behind subapical constriction, abruptly widened at extreme base; in profile (Fig. 1), slightly, evenly convex; pleuron with dorsal, posterolateral excavation above lateral prominence and deep, posterior, submarginal sulcus; punctation dense on dorsal midline, sparse laterally, slightly more dense on pleuron; each puncture with an elongate, acuminate white to aeneous scale; interspaces broad, smooth, shining; scales on pleuron not different from those on lateral portions of dorsum. *Elytra* (Figs. 1, 2): Humeri slightly prominent, sides broadly constricted in basal $\frac{1}{2}$, widened in posterior $\frac{1}{2}$; interspaces 1–3 flat, widened slightly posteriorly, not depressed at extreme base, separated by narrow, deep, punctate striae; interspace 4 depressed at extreme base, narrowed posteriorly to basal $\frac{1}{4}$, slightly curved and distinctly widened posteriorly; interspace 5 depressed at extreme base, abruptly inflated and strongly curved in basal $\frac{1}{4}$; interspaces 6–10 more nearly uniform in width and convexity, striae separating them shallower, more sparsely punctate; surface of interspaces 1–3 distinctly punctate on disc; these interspaces posteriorly, and other interspaces throughout, not obviously punctate; vestiture consists of elongate, narrow, recumbent, whitish to aenescent scales; vestiture dense on extreme base of interspaces 1 and 2, and on basal $\frac{1}{4}$ of interspace 3, sparse on more convex portions of other interspaces, slightly more dense posteriorly. *Pygidium* (Fig. 3): Convex, evenly rounded apically; with small apicodorsal emargination; exposed portion punctate, with elongate, acuminate scales. *Abdomen*: Sterna 1–5 subequal in length, flattened medially, with sparse, narrow setae medially, broader, acuminate, whitish scales laterally; posterior margin of sternum 5 unmodified. *Genitalia* (Fig. 4): Median lobe with sides subparallel, narrowed apically; endophallus bearing scattered denticles. *Legs*: Profemur about $1.4 \times$ broader than metafemur; distal tooth of pro-



Figs. 1-4. Adult male, *A. santarosae*, Santa Rosa National Park, Guanacaste Province, Costa Rica. 1, Habitus, lateral view. 2, Habitus, dorsal view. 3, Pygidium, dorsal view. 4, Median lobe of genitalia, dorsal view.

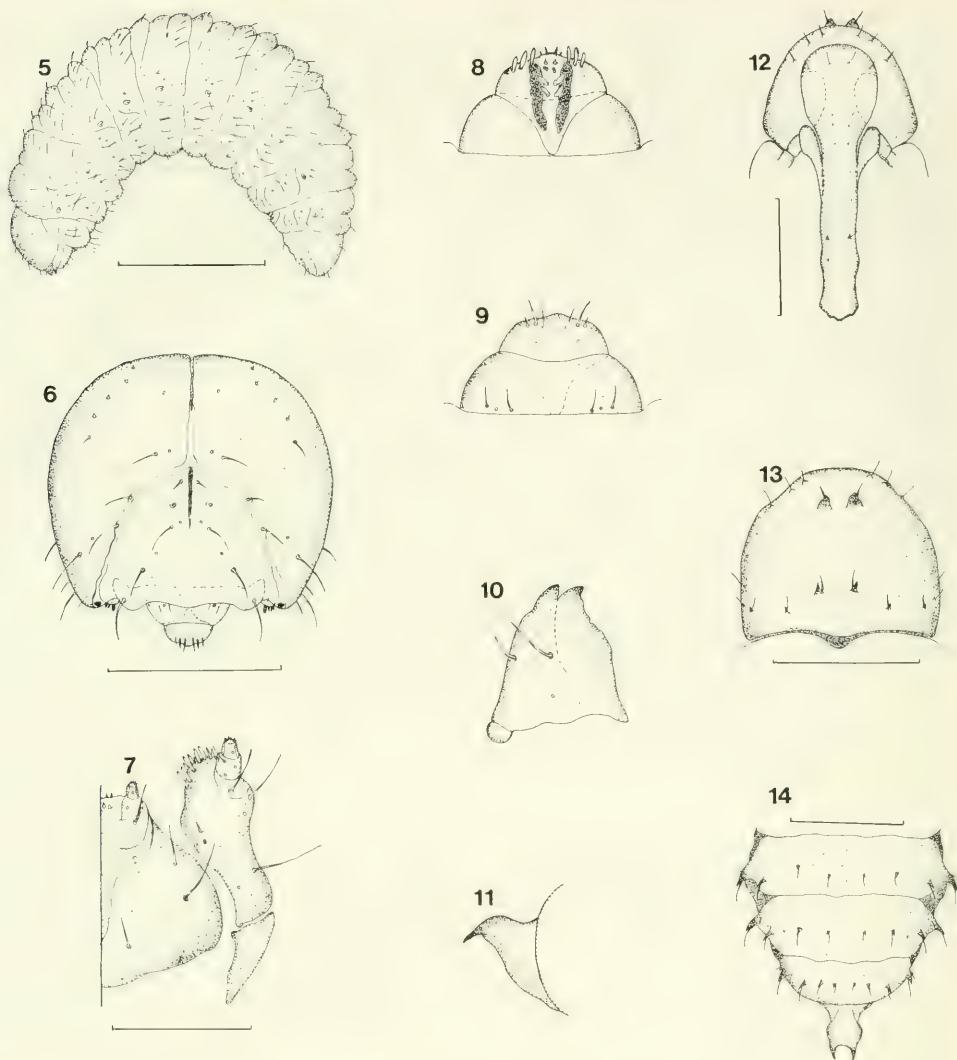
femur with serrate distal margin; protibia straight on dorsal margin, ventral margin with strong, obtuse, median, subapically subangulate prominence; apical mucro long, slender; metatibia with broader, longer, less abrupt median prominence on ventral margin, constricted and narrowed at apex; apical mucro short, curved, excavated.

Adult female.—*Length*: 3.7–5.2 ($m = 4.8$, $n = 15$) mm. *Width*: 1.7–2.6 ($m = 2.0$, $n = 15$) mm. *Rostrum*: Length 1.7–1.9 ($m = 1.85$, $n = 15$) $\times$ pronotal length, broadly, evenly curved from base to apex; portion distal to antennal insertions 36–41 ($m = 39$, $n = 15$) % of total rostral length. *Pygidium*: With subangulate apicomedian prominence. *Abdomen*: Sternum 5 narrowed and slightly prominent apicomediaally.

Larva (Figs. 5–10).—The following description is based on third instar larva. Terminology is that of Anderson (1947). *Body* (Fig. 5): Strongly curved; length ca. 4.5 mm. Asperities minute, tubercle-like, irregularly distributed on dorsal and ventral areas of body. Color white, except for reddish brown area on pronotum. *Head* (Fig. 6): Pale amber; width of head capsule 0.85–1.07 mm ($n = 8$). Basal article of antenna bearing subconical accessory appendage and four stout setae, one of which is slightly longer than others. Endocarina distinct, ca. $\frac{1}{2}$ length of frons. Epicranial suture less than $\frac{1}{2}$ length of head capsule. Four pairs of frontal setae present; seta 1 about $\frac{2}{3}$ length of seta 3; frontal setae 3, 4 and 5 long, slender, of about equal length. Two pairs of frontal sensilla, one pair located mesad of bases of frontal setae 3, another located ca. $\frac{1}{2}$ way between bases of setae 3 and

4. Five pairs of dorsal epicranial setae present; setae 1, 4 and 5 slender, nearly equal in length; setae 2 and 3 shorter than other dorsal epicranial setae, 2 slightly shorter than 3; setae 3 and 4 located either in or adjacent to frontal suture. Four pairs of short peg-like postcranial setae arranged in a slight arc, with lowermost located directly above dorsal epicranial seta 2. Three pairs of epicranial sensilla; one pair located $\frac{1}{2}$ way between postepicranial seta 3 and epicranial suture; one pair mesad of epicranial seta 1; third pair between epicranial setae 4 and 5. Lateral epicranial seta 1 about $\frac{2}{3}$ length of 2. Ventral epicranial setae 1 and 2 ca. equal in length. Clypeal setae (Fig. 9) slender; seta 1 slightly longer than 2; seta 2 located farther from anterior margin of frons than 1. One pair of clypeal sensilla; each member of pair located adjacent to anterior margin of frons, halfway between bases of setae 1 and 2. Three pairs of labral setae (Fig. 9); setae 1 and 2 ca. the same length but 2 stouter; seta 3 much shorter. Epipharynx (Fig. 8) bearing two pairs of anteromedian setae, innermost pair longer. Three pairs of stout anterolateral setae present. Labral rods stout, converging slightly posteriorly. Two groups of epipharyngeal sensory pores consisting of two pores in each group. Two pairs of short, stout epipharyngeal median spines present between labral rods. Mandibles (Fig. 10) with two teeth; bearing two long, slender setae of ca. same length. Maxillary palps with apical article (Fig. 7) nearly $\frac{2}{3}$ length of basal article, bearing several small elongate tubercles at apex; basal article with seta the length of which is ca. $\frac{2}{3}$ width of article. Stipital setae, 1, 3 and 4 long, slender, seta 1 longer than other two; seta 2 considerably shorter. Mala bearing 11 stout setae, 6 ventral and 5 dorsal. Labial palpus consists of two articles. Premental sclerite with long, stout posterior process. One pair of long, slender premental setae. Four pairs of glossal setae, two pairs short, stout, other two pairs slightly longer. Postmental setae long, slender; seta 3 shorter. *Thorax* (Fig. 5) (setae described on one side of the body only): Pronotum bearing 10 long setae and one short seta. Prodorsal seta long, slender. Five postdorsal setae present; setae 1, 3 and 5 distinctly longer than 2 and 4. Three spiracular setae present, two of which are of equal length and longer than the third. Epipleural lobe bearing one long seta. Two long prothoracic pleural setae; one pleural seta on each of meso- and metathorax. Four long pedal setae. Sternal seta about $\frac{2}{3}$ length of pedal setae. *Abdomen* (Fig. 5): First seven abdominal segments bearing three dorsal folds; segment VIII with two well-defined folds. Prodorsum of each segment bearing a moderately long seta. Five postdorsal setae present; setae 1, 3 and 5 much longer than 2 and 4. Two spiracular setae; seta 2 at least $3\times$ longer than 1. Epipleurum bearing one long seta and another ca. $\frac{1}{2}$ as long. One moderately long pleural seta and an equally long pedal seta. Two short, inconspicuous pedal setae on each segment. Anus subterminal, surrounded by four lobes; one long ventral seta in area of anterior lobe; other lobes apparently without setae. Elsewhere on segment IX two short setae present dorsally near anterior margin of segment; seven setae laterally near apex of segment. Spiracles bicameral, air tubes with 5 or 6 annuli.

Pupa (Figs. 11–14).—Terminology of pupal characters follows Burke (1968). *Body*: Length 4.9–6.0 mm ($n = 8$). *Head* (Fig. 12): Supraorbital setae fine, straight to slightly curved or strongly bent near apices, each ca. $\frac{2}{3}$ length of frontal seta; borne on supraorbital ridge. Frontal setae stout, straight; each borne on summit of low tubercle; tubercles separated by distance equal to slightly more than length of a seta. *Rostrum* (Fig. 12): Extending to apices of tarsi of mesothoracic legs in



Figs. 5-14. Larva and pupa of *A. santarosae*. 5, Larva, lateral view. 6, Larva, frontal view of head capsule. 7, Larva, ventral view of labium and left maxilla. 8, Larva, epipharynx. 9, Larva, clypeus and labrum, dorsal view. 10, Larva, mandible. 11, Pupa, lateral view of abdominal segment IX. 12, Pupa, head, rostrum and ventral view of prothorax. 13, Pupa, prothorax, dorsal view. 14, Pupa, terminal abdominal segments, dorsal view. Line accompanying Fig. 5 = 2 mm; Fig. 6 = 0.5 mm; Fig. 7 = 0.25 mm; Figs. 8, 9, 10, 11 = greatly enlarged; Fig. 12 = 1 mm; Fig. 13 = 1 mm; Fig. 14 = 1 mm.

male, slightly past these in female. One pair of straight distirostral setae; each seta borne subapically on small, pointed tubercle; length of each seta equal to ca. $\frac{1}{5}$ width of rostrum. An additional pair of shorter setae located distad of distirostrals; each seta borne on minute, acutely pointed tubercle. Three pairs of fine, straight to slightly curved basirostral setae, proximal pair somewhat stouter; not borne on tubercles or borne on minute ones; sometimes irregularly spaced so that they do not appear to be paired. *Prothorax* (Fig. 13): Prothoracic depression absent. Pronotal setae usually straight, sometimes feebly curved; setae on anterior margin

of pronotum stouter than posterior ones. Anteromedian setae each borne subapically on anterior face of large, obtusely pointed to broadly rounded tubercle; length of each seta equal to slightly more than height of tubercle. Tubercles separated by distance equal to ca. width of a tubercle. Three pairs of anterolateral setae, each of which is borne on summit of low, flat-topped tubercle; tubercle 2 usually located slightly closer to tubercle 1 than to 3. Posteromedian setae each borne near base of sharply pointed tubercle; tubercles separated by distance equal to about $2 \times$ height of tubercle. Four pairs of posterolateral setae, each of which is borne at or near base of sharply pointed tubercle; tubercles decreasing in size laterally, outermost sometimes rounded dorsally. *Mesonotum*: With three pairs of straight mesonotal setae; two inner setae, each borne at base of large sharply pointed tubercle; outer seta higher on summit of slightly rounded tubercle or at base of a small sharply pointed one. Anteronotal setae absent. *Metanotum*: Bearing three pairs of usually straight setae, each of which is borne at base of sharply pointed tubercle; about equally separated from each other. *Abdomen* (Fig. 14): With three pairs of discotergal setae which increase in length laterally; discotergal seta 1 on terga I–IV or V borne on summit of low, rounded tubercle, on remaining terga located at base of small, sharply pointed tubercle; discotergals 2 and 3 borne at bases of sharply pointed tubercles (except occasionally discotergal 1 sessile on tergum I) that increase gradually in size posteriorly. Laterotergal setae 1 and 2 present on each of terga I–VIII; seta 1 minute, borne at base of small sharply pointed tubercle on all terga; seta 2 borne subapically on sharply pointed tubercle on terga I–VIII, tubercles increase gradually in size posteriorly. Anteronotal setae absent. Spiracles present on abdominal segments I–VI, well developed on I–V, poorly developed on VI. One pair of laterosternal setae on each segment located directly below laterotergal seta 2; length of seta ca. $\frac{1}{4}$ length of laterotergal seta 2. Sub-laterosternal setae absent. Segment IX bearing a pair of sharply pointed posterior processes (Fig. 11), which in side view point slightly to strongly downward; setae absent on segment.

DISCUSSION

The paratypes from Panama differ from the Costa Rican and Venezuelan specimens in being slightly more robust and darker. The Panamanian specimens are black and shining, but the Costa Rican and Venezuelan ones are brownish (many of them are teneral). The specimens from Panama also have shallower punctures and sulci and slightly less dense vestiture on the prothorax and elytra.

Adults of *A. santarosae* may be distinguished from all other known *Anthonomini* by the distinctive shape of the elytra (Fig. 2), which are enlarged posteriorly, and by the 4th elytral interspace being narrowed at its base and widened and curved posteriorly. The 4th elytral interspace also has a dense vestiture of elongate scales in its basal $\frac{1}{3}$. Also distinctive is the metatibia of the male, which has a median prominence on the ventral margin and is constricted and narrowed at the apex. In addition, *A. santarosae* differs from the related *A. grandis* by its narrower form, larger eyes in comparison to the head, and more strongly sinuate inner margins of the male tibiae. These differences also distinguish *A. santarosae* from species of the subgenus *Anthonomorphus*.

The larva of *A. santarosae* keys in Ahmad and Burke (1972) to the section containing *A. grandis*, *A. fulvus* LeConte, *A. texanus* Dietz and *Lonocophorus fusiformis* Champion. It closely resembles the larvae of these species indicating

that all are fairly closely related to each other. A possible sister-group relationship between *A. grandis* and the subgenus *Anthonomorphus* was recently indicated in studies by Clark and Burke (in press). Studies are underway to test these hypotheses of relationships with further comparisons of the adult and immature stages of *A. grandis* and the species of *Anthonomorphus*, *L. fusiformis* and other species of *Loncophorus*, and *A. santarosae*.

The larva of *A. santarosae* differs from those of *A. fulvus* and *A. texanus* by the lack of pigmentation on the pleural lobes and body tubercles. The hosts of the latter two North American species also differ; larvae of *A. fulvus* develop in flower buds of *Callirhoe* and *Sphaeralcea* spp., while larvae of *A. texanus* develop in buds of *Sphaeralcea* spp. (Burke et al., 1984). If the color of the head capsule is deemphasized as a character, *A. santarosae* would trace to the couplet containing *L. fusiformis* with which it agrees in having four glossal setae as opposed to two in *A. grandis*. The host of *L. fusiformis* is *Ceiba* sp. (Bombacaceae). The larva of *A. santarosae* has a pale amber head capsule as compared to the light yellowish brown one of *A. grandis*. In addition to having only two glossal setae, *A. grandis* differs from *A. santarosae* in its host plants, not being known to develop in *Bombacopsis*.

The pupa of *A. santarosae* supports relationships determined by adult and larval characters. It is distinguished from pupae of *A. fulvus*, *A. texanus*, *A. grandis* and *L. fusiformis* by having three instead of five pairs of discotergal setae. There is occasionally an extra tubercle without a seta in the discotergal series, indicating that the three discotergal setae condition of *A. santarosae* represents a reduction from a basic four or five pairs of setae.

The assignment of this species to the genus *Anthonomus* was made only after consideration of its relationships with the species assigned to *Loncophorus* and *Atractomerus*. Champion (1903) characterized the species of *Loncophorus* [including species later transferred to *Atractomerus* by Voss (1944)] as "mostly of large size and navicular form," and Pierce (1916: 467) used presence of postocular lobes on the prothorax to distinguish his *Loncophorini* (including only the genus *Loncophorus*) from *Anthonomini*. Since the new species is not "navicular" in form and does not have postocular lobes it is provisionally placed in *Anthonomus*. Relationships of *A. santarosae* and the species now in *Loncophorus* and *Atractomerus* will receive further consideration in ongoing studies.

D. H. Janzen writes that "the host flower buds are aborted from the crowns of large trees (up to 30 m high) and land on the litter below. They are 1.5–3.0 cm long at this time and quickly dry into a hard case, with the larva feeding inside. Bud fall is in February, the first half of the 5 to 6-month dry season. The host tree is leafless. There is no hint of a second generation after the adults eclose. Ecdysis is through a hole cut in the side of the bud in late February and early March. The beetle is normally only one per bud, and at least three species of hymenopterous parasitoids have been removed from [*A. santarosae*] larvae. They eclose as adults through the side of the flower bud well after it has fallen from the tree."

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Janzen, University of Pennsylvania, Philadelphia; Luis J. Joly T., Facultad de Agronomía, Universidad Central de Venezuela, Maracay; Charles W. O'Brien, Florida A&M University, Tallahassee; and D. R. Whitehead, Systematic Entomology Laboratory, Agricultural Research Service, Washington, D.C. This paper is published as Alabama Agricultural Experiment Station Journal No. 15-85919, and Texas Agricultural Experiment Station, TA 21036.

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NOTES ON THE DISTRIBUTION AND ABUNDANCE OF
DERMAPTERA AND STAPHYLINIDAE (COLEOPTERA)
IN SOME COSTA RICAN CACAO PLANTATIONS

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Abstract.—The distribution and abundance of Staphylinidae (Coleoptera) and Dermaptera were studied in experimental microhabitats (rotting banana tree trunk sections, cacao pod husk-halves, cacao leaf litter, hanging cups filled with leaf litter) within two markedly distinct cacao plantation habitats in Costa Rica over a one-year period. Additional collections of both groups were taken in other cacao plantations. Distinctive patterns of distribution of both Staphylinidae and Dermaptera were found. Overall, Dermaptera were more abundant in rotting cacao pod husk-halves than in banana tree trunk sections, and the opposite true for Staphylinidae. Staphylinidae were markedly more abundant in the exposed cacao plantation in the dry season than in the forest, and the opposite true for Dermaptera. During the subsequent rainy seasons, these patterns were reversed. Virtually all samples were “dominated” by two species of Staphylinidae (always the same species) and three species of Dermaptera. Individual microhabitat pieces commonly contained both Dermaptera and Staphylinidae. Percentage (%) occupancy levels of microhabitats varied greatly with habitat and season for both groups. Overall, however, there was no statistically significant difference in the mean abundance of both groups, for both rotting banana tree trunk sections and cacao pod husk-halves, between the two habitats studied.

In this paper I report patterns of distribution and abundance for two groups of largely cryptozoic organisms (sensu Allee et al., 1949), Dermaptera and Staphylinidae (Coleoptera), in experimental “microhabitats” in some Costa Rican cacao (“cocoa”) plantation habitats. Dermaptera and staphylinids are considered together in this paper since representatives of both groups frequently occur together in rotting organic debris in tropical habitats. The survey of insects described in this paper was based in large part upon the previous observation that Dermaptera species in Costa Rican cacao plantations often vary greatly in abundance among different microhabitats and times of the year (Young, 1984a). Relatively few studies have examined seasonal and microhabitat patterns of abundance in tropical cryptozoic insects and other arthropods (e.g. Lieberman and Dock, 1982; Irmeler, 1979; Legner et al., 1981; Puig, 1980; Young, 1982, 1983a, b, 1984a). Phenological patterns of Staphylinidae have been documented for temperate-zone habitats (e.g. Levesque and Levesque, 1984; O. P. Young, 1984), but little has been documented for neotropical species.

MATERIALS AND METHODS

These studies were conducted at the following Costa Rican cacao plantation localities: (1) "Finca La Tigra," near La Virgen (10°23'N, 84°07'W; 220 m elev.), Sarapiquí District, Heredia Province; (2) "C.A.T.I.E." at Turrialba (9°55'N, 87°02'W; 600 m elev.), Cartago Province; (3) "Finca Experimental La Lola," near Siquirres (10°06'N, 83°30'W; about 50 m elev.), Limón Province. The most extensive, systematic studies were conducted at the "La Lola" locality, where a short but intense dry season ("veranillo") usually occurs within February and March each year (Fig. 1).

The "La Tigra" and "Turrialba" studies were limited to checking replicated microhabitats during the dry season (1981 and 1982) for dermapterans and staphylinids. Insects were collected from various types of rotting, organic litter (banana tree trunk sections, cacao pod husks, cacao leaf litter, and plastic cups filled with leaf litter and suspended in cacao trees) (see also Young, 1982, 1983a, b, 1985). The "La Lola" study (1984) compared species and their numbers for dermapterans and staphylinids in rotting banana trunk sections and cacao pod husks split in half lengthwise and distributed in two adjacent but markedly different cacao habitats. These two habitats, a "cacao forest" (abandoned cacao plantation), and a well-kept "cacao plantation" were very different in terms of the degree of permanent shade cover and the ground-cover vegetation beneath the cacao trees (Fig. 2). In the "cacao forest" a dense shade cover over the ground cover was provided by both self-shading cacao trees (50–60 years old and unpruned) and an overstory of principally *Huara crepitans* Linnaeus (Euphorbiaceae) (Fig. 2). The relatively broken and uneven shade cover in the adjacent "cacao plantation" habitat consisted chiefly of *Erythrina* sp. (Fabaceae); here, cacao trees, although of the same cultivated variety ("Matina") and age as the trees in the "cacao forest," were frequently pruned thereby reducing shade cover throughout the year. The general result of these habitat differences is that during the dry season, the *H. crepitans* shade in the cacao forest is greatly reduced due to the intense leaf-drop and the *Erythrina* sp. shade in the plantation less so.

In the "La Lola" study, three censuses of Dermaptera and Staphylinidae in rotting cacao pod husk-halves, banana tree trunk sections (see figures in Young, 1983a), leaf litter, and intact (whole) rotting cacao pods either on the ground or still attached to branches, were taken at widely-scattered intervals within a twelve-month period corresponding to "dry season" (March), "mid-rainy season" (August), and "late rainy season" (November). At each census, the following "microhabitat" pieces were collected from each of the two habitats (forest and plantation): 60 banana tree trunk sections, 75 cacao pod husk-halves, 350 cacao leaves, 35 arboreal rotting cacao pods, and 35 intact pods rotting on the ground beneath cacao trees. Approximately three months prior to each census, 125 banana trunk slices and 150 pods husk-halves were distributed in groups of five in each of the two habitats, their locations randomized by number-coded cacao trees. An additional five 1 × 1-meter wooden frames were similarly distributed in each habitat and filled with cacao leaves. Intact pods on the ground, and pods rotting on the trees, happened upon at each census were also examined for insects. Substrates were brought to a field station for removal of insects and recording of numbers per piece. From these observations a voucher collection was generated

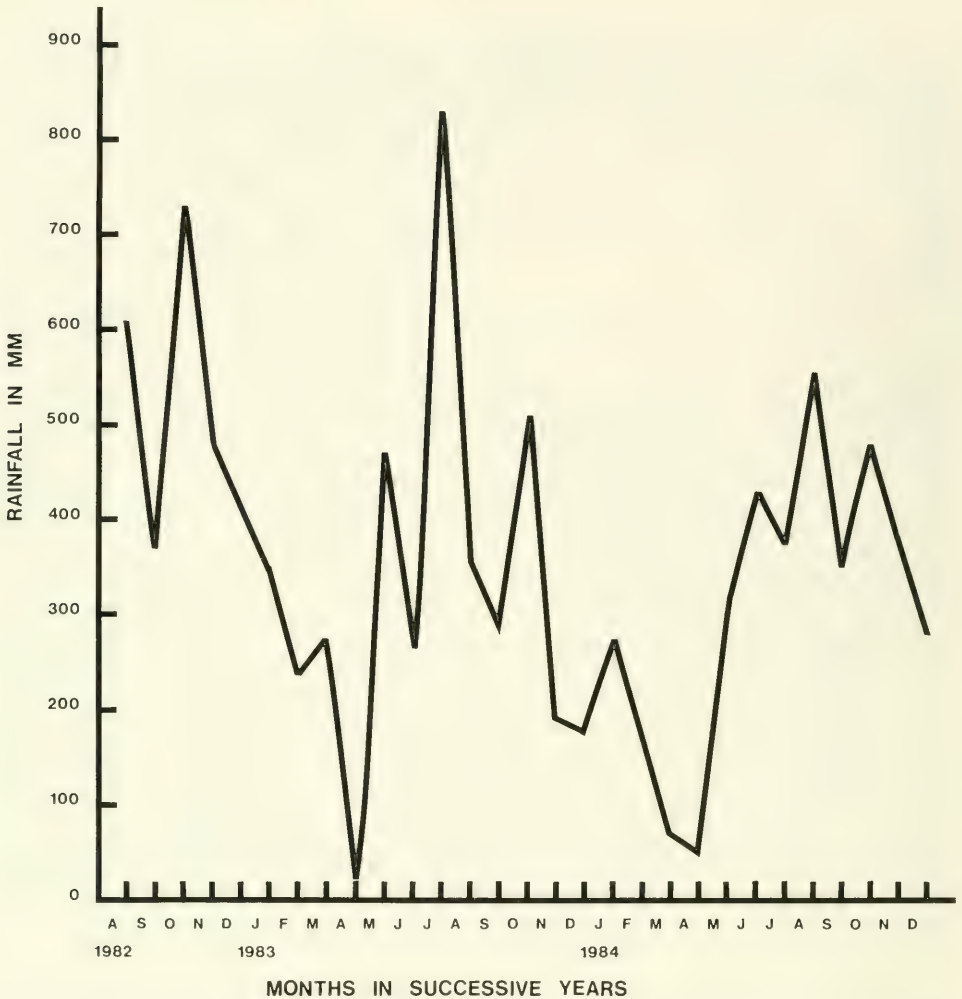


Fig. 1. Monthly rainfall pattern (in mm) for several successive years, including the study period, at "Finca Experimental La Lola." A dry season occurs each year between February and April.

and subsequent identifications to genera and species, when possible, were undertaken. A similar approach was used for collections at "La Tigra" and "Turrialba."

RESULTS

A preliminary census of Staphylinidae alone for the dry season period at three widely scattered cacao plantations indicated that two species, *Belonuchus* nr. *mimeticus* and *Piestus sulcatus*, were the most abundant representatives at "La Lola" and "Turrialba" (Table 1). Most interesting from this preliminary survey was the discovery of *B.* nr. *mimeticus* in arboreal cup leaf litter, even though very scarcely so (Table 1). Thus *B.* nr. *mimeticus* occurred at more than one stratum within the cacao plantation habitat. *Parosus* sp. no. 1, exceedingly scarce species,



Fig. 2. Contrasting cacao habitats studied. Above: "cacao forest" showing cacao trees and trunk of a *Huara crepitans* (Euphorbiaceae) overstory tree. Below: open "cacao plantation" habitat at "La Lola." Note exposed cacao trees and grassy ground cover in the cacao plantation habitat.

Table 1. Summary of a preliminary survey of Staphylinidae associated with cryptozoic-type microhabitats at three cacao plantations in Costa Rica during dry seasons.

Locality	Census Date	Substrate Examined and % of Occupancy	Species	Numbers	% of Total Sample
"Turrialba" (C.A.T.I.E.)	17 Feb. 1981	banana tree trunk sections (5/300 = 1.7% occupied)	<i>Piestus sulcatus</i> Grav.	27	49.1%
			<i>Belonuchus</i> nr. <i>mimeticus</i> Sharp	14	25.5%
			Aleocharinae sp. no. 1	9	16.4%
			<i>Medon</i> sp. no. 1	2	3.6%
		arboreal cup litter (1/22 = 4.5% occupied)	<i>Stilomedon</i> sp. no. 1	1	1.8%
			Aleocharinae sp. no. 3	1	1.8%
			<i>B.</i> nr. <i>mimeticus</i>	1	1.8%
"La Lola"	10 Feb. 1981	banana tree trunk sections (48/240 = 20.0% occupied)	<i>B.</i> nr. <i>mimeticus</i>	33	33.7%
			<i>P. sulcatus</i>	65	66.3%
	11 Mar. 1982	banana tree trunk sections (2/240 = 0.8% occupied)	<i>B.</i> nr. <i>mimeticus</i>	30	69.8%
			<i>P. sulcatus</i>	12	27.9%
			<i>Medon</i> sp. no. 1	1	2.3%
"La Tigra"	5 Feb. 1981	banana tree trunk sections (1/240 = 0.4% occupied)	<i>Parosus</i> sp. no. 1	1	100.0%

was found at “La Tigra” and not at the other two localities. Previous collections of insects from rotting banana tree trunk sections in “La Lola” cacao plantation habitats included several species of carabid beetles: *Perigona laevigata* Bates, *Pentagonica maculicornis* Bates, and *Platynus orbicollis* Chaudoir. While carabids were not collected in the present study, their numbers appeared to be very low in all samples.

About 56% of all Dermaptera (167/301) and about 54% (74/138) of all Staphylinidae collected in the “La Lola” study came from the plantation habitat. Such data suggest an even split of both groups of insects between the two habitats. Bias in such data may come from the preponderance of dermapterans over staphylinids in samples, since about 69% of all insects collected from banana tree trunk sections and cacao pod husk-halves combined were Dermaptera (301/439 insects).

For both habitats combined, 68.2% (204/299) of Dermaptera occurred in the cacao pod husk-halves, whereas the reverse pattern was true for Staphylinidae, in which 65.9% (91/138) occurred in the banana tree trunk sections. But these patterns change with habitat: for Dermaptera, 84.4% of all individuals collected occurred in cacao pod husk-halves in the “cacao forest” habitat; for Staphylinidae, 83.8% (62/74) occurred in banana tree trunk sections in the “cacao plantation” habitat. For both Dermaptera and Staphylinidae (Tables 2 and 3), there were no significant differences in the mean abundance of all species (summed) between forest and plantation habitats for population in rotting banana tree trunk sections (Student's $t = 1.224$, $P > 0.05$ for Dermaptera; $t = 1.126$, $P > 0.05$ for Staphylinidae). No significant differences were found for both groups in rotting cacao pod husks as well ($t = 0.834$, $P > 0.05$ for Dermaptera; $t = 0.899$, $P > 0.05$ for Staphylinidae). In spite of what appeared to be large differences in total abundances between habitats for a given microhabitat study (Tables 2 and 3), markedly different sample sizes obliterated any significant differences in the samples collected.

Percentages (%) of “occupancy” for banana tree trunk sections and cacao pod husk-halves also change with tropical season. Whereas about 40% of banana tree trunk sections were occupied by Dermaptera in the dry season census for the “cacao forest” and only 13.3% for the “cacao plantation,” about the same percentages of occupancy were observed for cacao pod husk-halves between the two habitats (13.3% of husks in the “cacao forest” and 14.7% occupied in the “cacao plantation,” respectively). Overall occupancy dropped sharply by the mid-rainy season (August) for banana tree trunk sections, but not so for cacao pod husk-halves: about 13.3% of the banana tree trunk sections were occupied by Dermaptera in the forest and 3.3% in the plantation. But more than three times the number of cacao pod husk-halves in the plantation had Dermaptera than in the forest (30.7% occupancy in the plantation and 10.7% occupancy in the forest habitat). This pattern for Dermaptera remained the same for the late-rainy season census (November): 13.3% of banana tree trunk sections were occupied in the “cacao forest” and none were occupied in the “cacao plantation.” Almost four times the number of cacao pod husk-halves were occupied in the plantation than in the forest habitat at this time (44.0% occupancy for the “cacao plantation” and 12.0% for the “cacao forest”).

For Staphylinidae, close to three times the number of banana tree trunk sections were occupied in the plantation than in the adjacent forest (41.7% and 15.0% respectively) during the dry season (March) census. About twice the number of

Table 2. Distribution and abundance of Dermaptera from replicated "microhabitat" substrates in two contrasting and adjacent cacao "habitats" in the eastern lowlands of Costa Rica for one complete cycle of dry season and rainy seasons.

Census Date	Species	Banana Tree Trunk Sections (Microhabitats) (N = 60 per habitat)			Cacao Pod Husk-Halves Microhabitats (N = 75 per habitat)			Total Insects; Sub- strates Combined
		N	% Total Sample	% Microhabi- tats Occupied	N	% Total Sample	% Microhabi- tats Occupied	
8-11 March 1984	"Cacao Forest"							
	<i>Carcinophora americana</i> (Beauvois)	14	29.2%	13.3%	10	27.0%	4.0%	24
	<i>C. festiva</i> (Burr)	22	45.8%	20.0%	19	70.4%	6.7%	41
	<i>C. gagatina</i> (Klug)	12	25.0%	6.7%	8	21.6%	2.7%	20
	Total	48		40.0%	37		13.3%	85
	"Cacao Plantation"							
	<i>C. americana</i>	6	25.0%	3.3%	12	35.3%	4.0%	18
	<i>C. festiva</i>	3	12.5%	3.3%	7	20.6%	2.7%	10
	<i>C. gagatina</i>	5	20.8%	1.7%	8	23.5%	4.0%	13
	<i>Anisolabis maritima</i> (Bonelli)	7	29.2%	3.3%	5	14.7%	2.7%	12
	<i>Euborellia annulipes</i> (Lucas)	3	12.5%	1.7%	2	5.9%	1.3%	5
Total	24		13.3%	34		14.7%	58	
8-12 Aug 1984	"Cacao Forest"							
	<i>C. americana</i>	1	9.1%	1.7%	2	14.3%	1.3%	3
	<i>C. festiva</i>	6	54.5%	6.7%	11	78.6%	8.0%	17
	<i>C. gagatina</i>	3	27.3%	3.3%	1	7.1%	1.3%	4
	<i>E. annulipes</i>	1	9.1%	1.7%	0	—	—	1
	Total	11		13.4%	14		10.6%	25
	"Cacao Plantation"							
	<i>C. americana</i>	0	—	—	12	32.4%	10.7%	12
	<i>C. festiva</i>	1	50.0%	1.7%	18	48.6%	13.3%	19
	<i>C. gagatina</i>	1	50.0%	1.7%	3	8.1%	4.0%	4
	<i>A. maritima</i>	0	—	—	2	5.4%	1.3%	2
<i>E. annulipes</i>	0	—	—	2	5.4%	1.3%	2	
Total	2		3.4%	37		30.6%	39	

Table 2. Continued.

Census Date	Species	Banana Tree Trunk Sections (Microhabitats) (N = 60 per habitat)			Cacao Pod Husk-Halves Microhabitats (N = 75 per habitat)			Total Insects; Sub- strates Combined
		N	% Total Sample	% Microhabi- tats Occupied	N	% Total Sample	% Microhabi- tats Occupied	
12-16 Nov 1984	"Cacao Forest"							
	<i>C. americana</i>	2	16.7%	3.3%	1	8.3%	1.3%	3
	<i>C. festiva</i>	8	66.7%	8.3%	10	83.3%	9.3%	18
	<i>C. gagatina</i>	2	16.7%	1.7%	1	8.3%	1.3%	3
	Total	12		13.3%	12		11.9%	24
	"Cacao Plantation"							
	<i>C. americana</i>	0	—	—	23	32.9%	12.0%	23
	<i>C. festiva</i>	0	—	—	—	—	—	—
	<i>C. gagatina</i>	0	—	—	31	44.3%	21.3%	31
	<i>Anisolabis maritima</i>	0	—	—	9	12.9%	8.0%	9
	<i>Euborellia annulipes</i>	0	—	—	7	10.0%	2.7%	7
	Total	0		—	70		44.0%	
Forest—total insects (all species)		71			63			
Forest—total % occupancy		40/180 = 22.2%			27/225 = 12.0%			301
Plantation—total insects		26			141			
Plantation—total % occupancy		10/180 = 5.6%			67/225 = 29.8%			

Table 3. Distribution and abundance of Staphylinidae (Coleoptera) from replicated "microhabitat" substrates in two contrasting and adjacent cacao "habitats" on the eastern lowlands of Costa Rica for one complete cycle of dry season and rainy seasons.

Census Date	Species	Banana Tree Trunk Sections (Microhabitats) (N = 60 per habitat)			Cacao Pod Husk-Halves Microhabitats (N = 75 per habitat)			Total Insects; Sub- strates Combined
		N	% Total Sample	% Microhabi- tats Occupied	N	% Total Sample	% Microhabi- tats Occupied	
8-11 March 1984	"Cacao Forest"							
	<i>Belonuchus</i> nr. <i>mimeticus</i> Sharp	6	46.2%	5.0%	22	88.0%	16.0%	28
	<i>Piestus sulcatus</i> Grav.	4	30.8%	6.7%	3	12.0%	4.0%	7
	<i>Stilomedon</i> sp. #1	1	7.7%	1.7%	0	—	—	1
	<i>Medon</i> sp. #1	2	15.4%	1.7%	0	—	—	2
	Total	13		15.1%	25		20.0%	38
	"Cacao Plantation"							
	<i>B. nr. mimeticus</i>	23	43.4%	23.3%	6	60.0%	6.7%	29
	<i>P. sulcatus</i>	25	47.2%	13.3%	4	40.0%	4.0%	29
	<i>Medon</i> sp. #1	5	9.4%	5.0%	0	—	—	5
	Total	53		41.6%	10		10.7%	63
8-12 Aug 1984	"Cacao Forest"							
	<i>B. nr. mimeticus</i>	7	63.6%	10.0%	5	83.3%	4.0%	12
	<i>P. sulcatus</i>	4	36.4%	6.7%	1	16.7%	1.3%	5
	Total	11		16.7%	6		5.3%	17
	"Cacao Plantation"							
	<i>B. nr. mimeticus</i>	1	14.3%	1.7%	1	50.0%	1.3%	2
	<i>P. sulcatus</i>	3	42.9%	5.0%	1	50.0%	1.3%	4
	<i>Medon</i> sp. #1	2	28.6%	3.3%	0	—	—	2
	<i>Apocellus</i> nr. <i>barbatus</i> Sharp	1	14.3%	1.7%	0	—	—	1
	Total	7		11.7%	2		2.6%	9
	12-16 Nov 1984	"Cacao Forest"						
<i>B. nr. mimeticus</i>		4	80.0%	6.7%	4	100.0%	2.7%	8
<i>P. sulcatus</i>		1	20.0%	1.7%	0	—	—	1
Total		5		8.4%	4		2.7%	9

Table 3. Continued.

Census Date	Species	Banana Tree Trunk Sections (Microhabitats) (N = 60 per habitat)			Cacao Pod Husk-Halves Microhabitats (N = 75 per habitat)			Total Insects; Sub- strates Combined
		N	% Total Sample	% Microhabi- tats Occupied	N	% Total Sample	% Microhabi- tats Occupied	
		"Cacao Plantation"						
	<i>B. nr. mimeticus</i>	2	100.0%	3.3%	0	—	—	2
	<i>P. sulcatus</i>	0	—	—	0	—	—	0
	Total	2		3.3%	0			2
		29			35			
Forest—total insects (all species)								
Forest—total % occupancy		24/180 = 13.3%			21/225 = 9.3%			138
Plantation—total insects		62			12			
Plantation—total % occupancy		34/180 = 18.9%			10/225 = 4.4%			

Table 4. Comparative abundances of Dermaptera species among tropical season censuses, for both habitats and microhabitat-types combined.

Species	Numbers of Individuals in Different Seasons:			Subtotal Rainy Season	Overall Total	Species % of Total Sample
	Dry Season	Mid-rainy Season	Late-rainy Season			
<i>Carcinophora festiva</i> (Burr)	58	36	18	54	112	36.4%
<i>C. americana</i> (Beauvois)	42	15	26	41	83	26.9%
<i>C. gagatina</i> (Klug)	33	8	34	42	75	24.4%
<i>Anisolabis maritima</i> (Bonelli)	12	2	9	11	23	7.5%
<i>Euborellia annulipes</i> (Lucas)	5	3	7	10	15	4.9%
Totals by seasons:	150	64	94			
% total by seasons:	48.7%	20.8%	30.5%			

cacao pod husk-halves were occupied in the forest than in the plantation at the same time of the year (20.0% and 10.7%, respectively), a reverse pattern from banana tree trunk section occupancy. While overall levels of occupancy for both banana tree trunk sections and cacao pod husk-halves were dramatically reduced at the mid-rainy season census, so too were differences between habitats: for banana tree trunk sections, 16.7% occupied in the forest and 11.7% in the plantation; for cacao pod husk-halves, 5.3% occupied in the forest and 2.7% in the plantation. Sample sizes were also reduced in the late-rainy season, although almost twice the number of banana tree trunk sections were occupied in the forest than in the plantation (8.3% and 3.3%, respectively). For cacao pod husk-halves, 2.7% were occupied in the forest and none were occupied in the plantation at this time.

Both "cacao forest" and "cacao plantation" habitats support similar arrays of species for both Dermaptera and Staphylinidae (Tables 2 and 3). Yet more than twice the number of dermapterans were found in exactly the same microhabitat samples than staphylinids for both habitats combined (i.e. 301 Dermaptera and 138 Staphylinidae) (Tables 2 and 3).

For Dermaptera in particular, more species were found in the March 1984 dry season census than in the two rainy season censuses, and within the dry season, a few more species were found in the "cacao plantation" than in the "cacao forest." Dermapterans and staphylinids frequently "co-occurred" in the same banana tree trunk sections and cacao pod husk-halves. In a few instances, two species of Dermaptera were found in the same microhabitat piece, although close to 90% of all such pieces examined for the entire study had only one species of Dermaptera per piece.

Staphylinidae exhibited markedly different levels of abundance among the three census periods. 59.4% of all Dermaptera in the dry season (85/143) occurred in the "cacao forest" habitat, 39.1% in the same habitat (25/64) in the mid-rainy season and only 25.5% in this habitat (24/94) at the late-rainy season census. Overall, 47.5% of all Dermaptera were from the single dry season census (143/301 insects). Only during the dry season census were Dermaptera markedly more abundant in the "cacao forest" habitat; in the other two censuses, these insects were more abundant in the "cacao plantation" habitat.

62.4% of all Staphylinidae during the dry season (63/101) occurred in the "cacao

Table 5. Comparative abundances of Staphylinidae species among tropical season censuses, for both habitats and microhabitat-types combined.

Species	Numbers of Individuals in Different Seasons:			Subtotal Rainy Season	Overall Total	Species % of Total Sample
	Dry Season	Mid-rainy Season	Late-rainy Season			
<i>Belonuchus</i> nr. <i>mimeticus</i> Sharp	57	14	10	24	812	58.7%
<i>Piestus sulcatus</i> Grav.	36	9	1	10	46	33.3%
<i>Medon</i> sp. no. 1	7	2	0	2	95	6.5%
<i>Stilomedon</i> sp. no. 1	1	0	0	0	1	0.7%
<i>Apocellus</i> nr. <i>barbatus</i> Sharp	0	1	0	1	1	0.7%
Totals by seasons:	101	26	11	37	138	
% total by seasons:	73.1%	18.8%	8.0%			

plantation.” But the subsequent pattern of abundance of staphylinids in the plantation habitat followed that for Dermaptera in the “cacao forest” habitat: 34.6% of staphylinids occurred in the plantation at the mid-rainy census, and only 18.2% occurred in the same habitat at the late-rainy season census. The dry season census alone accounted for 73.2% (101/138) of all Staphylinidae counted in the “La Lola” study, suggesting an even greater response to the dry season by staphylinids compared to dermapterans.

For both Dermaptera and Staphylinidae, the tropical dry season period (March) coincided with the greatest numbers found in rotting banana tree trunk sections and cacao pod husk-halves (Tables 4 and 5). For all three censuses, 0–2 individuals of Dermaptera (*Carcinophora festiva*, *C. americana*, and *C. gagatina* accounted for almost 90% of all individuals censused, and with *C. festiva* being the most abundant (Table 4). Two species of Staphylinidae, *Belonuchus* nr. *mimeticus* and *Piestus sulcatus*, comprised more than 90% of the entire sample size in the “La Lola” study (Table 5).

Both Dermaptera and Staphylinidae occurred in rotting, intact (whole) cacao pods on the ground and attached to branches (hanging pods) in both dry and rainy seasons (Table 6). While comparable numbers of Staphylinidae were found in forest and plantation habitats, about twice as many Dermaptera occurred in intact cacao pods in the plantation habitat than in the forest (Table 6). Two species of Staphylinidae, again *B. nr. mimeticus* and *P. sulcatus*, comprise the total fauna for this group in intact pods, both on the ground and still attached to branches (Table 6). The same three species of Dermaptera so abundant in the banana tree trunk sections and cacao pod husk-halves were the sole representatives of this group in the intact pods (Table 6). Occupancy levels of both groups were two or three times higher for pods on the ground than hanging cacao pods in the same stages of decay (Table 6). The overall percentages of total faunas (numbers of individuals) for both groups were not as high as they were for banana tree trunk sections and cacao pod husk-halves (Tables 4–6).

DISCUSSION

These data suggest that experimentally distributed rotting banana tree trunk sections and cacao pod husk-halves are equally suitable environments for various species of Dermaptera and staphylinid beetles. These substrates, as well as others

Table 6. Distribution of staphylinid beetles and Dermaptera in rotting substrates* in cacao habitats, other than banana tree trunk sections and pod husks.

Habitat	Date	Substrate-type	N	Staphylinids		Dermapterans	
				Species	Numbers	Species	Numbers
Cacao Forest	11 March 1984	hanging rotten pods	35	<i>Belonuchus</i> nr. <i>mimeticus</i> Sharp	2	<i>Carcinophora festiva</i> (Burri)	3
Cacao Plantation	11 March	hanging rotten pods	35	<i>B. mimeticus</i>	1	<i>C. festiva</i>	1
Cacao Forest	11 March	rotting pods on ground**	30	<i>Piestus sulcatus</i> Grav.	3	<i>Carcinophora gagatina</i>	
				<i>B. mimeticus</i>	2	(Klug)	1
Cacao Plantation	11 March	rotting pods on ground	30	<i>B. mimeticus</i>	1	<i>Carcinophora americana</i>	
				<i>P. sulcatus</i>	6	(Beauvois)	2
Cacao Forest	12 Aug 1984	hanging rotten pods	35	<i>B. mimeticus</i>	1	<i>C. gagatina</i>	6
Cacao Plantation	12 Aug	hanging rotten pods	35	none	—	<i>C. festiva</i>	4
Cacao Forest	12 Aug	rotting pods on ground	30	<i>P. sulcatus</i>	3	<i>C. festiva</i>	2
Cacao Plantation	12 Aug	rotting pods on ground	30	<i>B. mimeticus</i>	2	<i>C. festiva</i>	2
				<i>P. sulcatus</i>	4	<i>C. gagatina</i>	3
Cacao Forest	14 Nov 1984	hanging rotten pods	35	<i>B. mimeticus</i>	3	<i>C. festiva</i>	2
				<i>P. sulcatus</i>	4		
Cacao Plantation	14 Nov	hanging rotten pods	35	<i>B. mimeticus</i>	2	<i>C. festiva</i>	1
Cacao Forest	14 Nov	rotting pods on ground	30	<i>P. sulcatus</i>	5	none	
Cacao Plantation	14 Nov	rotting pods on ground	30	<i>P. sulcatus</i>	4	<i>C. festiva</i>	2
Total staphylinids in forest: 27 (individuals) 2 (species)							
Percent staphylinid occupancy of hanging rotten pods: 13/210 = 6.2% (habitats combined)							
Percent staphylinid occupancy of rotting pods on ground: 30/180 = 16.7% (habitats combined)							
Total staphylinids in plantation: 20 (individuals) 2 (species)							
Total Dermaptera in forest: 10 (individuals) 2 (species)							
Total Dermaptera in plantation: 21 (individuals) 2 (species)							
Percent Dermaptera occupancy of hanging rotten pods: 11/210 = 5.2% (habitats combined)							
Percent Dermaptera occupancy of rotting pods on ground: 30/180 = 16.7% (habitats combined)							
Percent staphylinids in dry season census: 15/44 = 34.1% (habitats combined)							
Percent Dermaptera in dry season census: 15/29 = 51.7% (habitats combined)							

* Individual pods with range of 0-3 individuals for both staphylinid beetles and Dermaptera.

** These are mature or near-mature pods, rotted largely by fungus diseases and cut off tree, intact by plantation workers.

studied, represent naturally occurring microhabitat for cryptozoic insects in Costa Rican cacao plantations. Yet the degree to which these microhabitats are occupied by staphylinids and dermapterans varies at different times of the year, and by habitat. Although I failed to find statistically significant differences in the mean abundance levels between habitats for both groups of insects, perhaps a result of small sample sizes, the data suggest that the *direction* of change in abundance between habitats is different between the groups.

The tendency for a few species to occur most commonly in samples, for both staphylinids and dermapterans, is not unexpected. The immature stages of a few species of ceratopogonid midges (Diptera) comprised the major portion of midge immatures in both rotting banana tree trunk sections and cacao pod husks at the same locality (Young, 1983a). As observed here for a few species of staphylinids, it was not uncommon to find the same ceratopogonid species in both terrestrial and arboreal microhabitats (Young, 1983a).

Cacao plantations in the Atlantic watershed region of Costa Rica generally have a broken, irregular shade cover and spongy leaf litter, factors perhaps related to the overall suitability for occupancy by staphylinids and dermapterans. Many cryptozoic insects require both shade and rotting organic debris (Allee, 1949).

Because dryness of decaying, terrestrial litter in cacao plantations is often a major determinant of insect distribution occupying litter substrates (e.g. Tawfik et al., 1976; Lieberman and Dock, 1982; Young, 1982, 1983a, b, 1984), differences in degree of shade cover, and its response to the tropical dry season between two adjacent or nearby habitats can generate different distributional patterns of cryptozoic insects, as indicated by my data. During the dry season, the shade trees in the forest habitat (chiefly *Huara crepitans*) drop their leaves, exposing both the understory cacao trees and ground cover to direct sunlight and drier conditions. Such an effect is less marked in the nearby cacao plantation (Young, 1984b). During the tropical dry season, rotting banana tree trunk sections retain moisture and become ecological micro-refuges for some insects (Young, 1983a). Because greater numbers of Dermaptera were found in rotting banana tree trunk sections in the forest habitat in the dry season than in the plantation, and the opposite pattern was found for staphylinids, it is evident that these groups respond in different ways to cycles of tropical seasonality.

A previous preliminary survey of Dermaptera between sunny and shaded habitats at "La Lola" revealed dramatic increases in densities in banana tree trunk sections in the dry season (Young, 1984a). In that study, three species, *Anisolabis maritima*, *Euborellia annulipes*, and *Marava triqueta* Hebard, together comprised about 25% of all samples from "La Tigra," "Turrialba," and "La Lola." Further comparative study of the natural history of both groups may elucidate why such markedly different distributional patterns exist. The general observation, also evident from my data, of both groups being less abundant in all substrates studies, during the rainy-season samples, suggests a more broad distribution of breeding populations of individual species at these times of the year. Both species number and abundance of individual species of insects often changes markedly in tropical habitats between seasons (e.g. Bates, 1945; Dobzhansky and Pavan, 1950; Owen and Chanter, 1970; Bowden, 1976; Buskirk and Buskirk, 1976; Irmiler, 1979; Denlinger, 1980; Young, 1980a, b, 1981).

During the dry season at "La Lola" relatively higher densities of various insects

occur in rotting banana tree trunk sections and cacao pod husk-halves (see also Young, 1982, 1983a, b). Some of these insects include Collembola, ants, and immature stages of various Diptera. Such insects may be suitable prey for Staphylinidae. Staphylinids may comprise one group of predatory insects capable of withstanding unfavorable periods of dryness in being generalist predators on various other organisms (e.g. Becker, 1975). Dermaptera in general exhibit considerable ecological flexibility in adapting to changing environmental conditions (e.g. Good, 1982; Miller, 1984), and therefore can thrive in moist microhabitats in both dry and rainy seasons in the tropics. While little is known about the precise feeding habitats of the staphylinids studied here, undoubtedly some, such as *Piestus* spp., are principally saprophagous or symbiotic wood-feeders (P. Hammond, pers. comm.). Others, such as *Belonuchus* and *Medon*, as well as the Aleocharinae represented in my samples, are predators on other arthropods (P. Hammond, pers. comm.). Being generalized scavengers on a broad range of rotting organic materials (e.g., O. P. Young, 1984 and several included references), dermapterans may be generalized decay-product feeders within the rotting microcosm of banana tree trunk sections and pod husk-halves. Dermaptera and Staphylinidae may use rotting banana tree trunk sections and cacao pod husks as breeding sites. The dermapteran *Carcinophora americana* (Beauvois) guards clutches of bright yellow eggs within the wall tissues of rotting cacao pod husks (based on one observation, A. M. Young).

The degree to which a microhabitat (substrate) is occupied by either staphylinids or dermapterans indicates the relative suitability of that microhabitat within the habitat. Thus the markedly high overall abundance of Dermaptera in the forest and their low abundance in the plantation suggests that the forest was more suitable for those species thriving in rotting banana stems. But the reverse was true for dermapterans in cacao pod husk-halves. Thus the net effect was an overall equal abundance of Dermaptera and between the two habitats, even though their distribution between the two microhabitat-types studied (banana tree trunk sections and cacao pod husks) was inversely-related.

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SEASONALITY AND TWO NEW SPECIES OF PANAMANIAN
XESTOCEPHALUS (HOMOPTERA: CICADELLIDAE)

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Abstract.—Two new species of *Xestocephalus*, *vittanotus* and *bifasciatus*, from the cloudforest at Guadalupe Arriba, Panama are described and illustrated. Their distribution in Panama is discussed. Temporal abundance as recorded from light trap samples is presented for five species of *Xestocephalus*.

The Republic of Panama has a rich *Xestocephalus* fauna, both in terms of species diversity and number of individuals. Wolda (1982) listed xestocephalines as representing the third largest leafhopper subfamily in terms of number of individuals collected in both a disturbed area and in an undisturbed forest. Although the new world *Xestocephalus* fauna is far from being fully realized, Panama is unique in the number of endemic species. Of the 42 *Xestocephalus* species reviewed by Cwikla (in press) for North and Central America, 38 percent are endemic to Panama. The Panamanian species of this subfamily were reviewed recently by DeLong et al. (1980), with additional species described by DeLong et al. (1983).

In this paper we describe two new species of *Xestocephalus* from Guadalupe Arriba, Panama with notes on their distribution. In addition, we discuss the temporal phenology of the five *Xestocephalus* species collected from this locality in 1984.

Methods.—Populations of leafhoppers were monitored at Guadalupe Arriba (82°33'13"W, 8°52'26"N) in the southwestern province of Chiriquí. This site is a cloudforest at 2100 meters and lies just inside the Panamanian national park, Volcán Baru. Although reliable rainfall data are not available for the area, there is a distinct "dry" season from January to April in which less rainfall is observed. Collections were made at this site using a modified Pennsylvania light-trap as described by Wolda and Fisk (1981). The trap was installed in early December 1983 and the contents were collected weekly until the end of 1984. The xestocephalines were identified and two species of *Xestocephalus* were determined to be previously undescribed.

Xestocephalus vittanotus Cwikla and Wolda, NEW SPECIES

Figs. 1-4

Length.—Male 4.7-5.1 mm, female 5.2-5.9 mm.

Structural features.—Crown slightly produced, head distinctly narrower than pronotum. Other features characteristic of genus.

Color.—Variable. Crown white with irregular light brown markings, broken obliquely transverse dark brown band present or absent on anterior margin. Face brown or white, V-shaped brown patch present or absent under each ocellus. Pronotum white and heavily marked with irregular brown patches, light brown median vitta usually present. Scutellum white or cream, disc sometimes with small light brown patch, anterior margins light brown. Forewing light brown, irregular dark brown and white patches throughout wing. Lateral aspect of thorax, legs and abdomen brown.

Male genitalia.—Pygofer with posterior margin produced, internal tooth-like processes directed medially. Plates with apex truncate. Aedeagus in lateral aspect with posterior margin under gonopore slightly concave, two pair of processes present, ventral processes long, directed laterally then turning posteriorly in lateral aspect, pair of small spine-like processes present above ventral processes, directed laterally, apex of shaft acute. Gonopore subapical. Styler apex narrow and curved, slight serration on heel.

Type-series.—Holotype ♂, Panama, Chiriquí, Guadalupe Arriba, 2100 meters, 8°52'26"N, 82°33'13"W, 25–31 January 1984, H. Wolda coll. Paratypes: 4 ♀ and 3 ♂ with same data as holotype except for 1 ♀ 21–27-XII-1983, 1 ♂ 28-XII-1983 and 1 ♂ 2–8-V-1984. All types deposited in the DeLong Collection, Ohio State University, except for 1 ♂ (28-XII-1983) and 1 ♀ (25–31-I-1984) paratypes deposited in the H. Wolda Collection.

Variation.—Dark brown maculations on the crown, pronotum and forewings vary between individuals in the type-series. The coronal markings also vary from light brown to dark brown.

Etymology.—Latin vitta (band) and the Greek notum (back) refer to the band on the pronotum.

Diagnostic features.—The species is related to *artarus* DeLong, Wolda, and Estribi and can be separated from it by the posterior margin of the aedeagal shaft under the gonopore being slightly concave in lateral aspect and the short spine-like aedeagal processes situated above the long ventral processes.

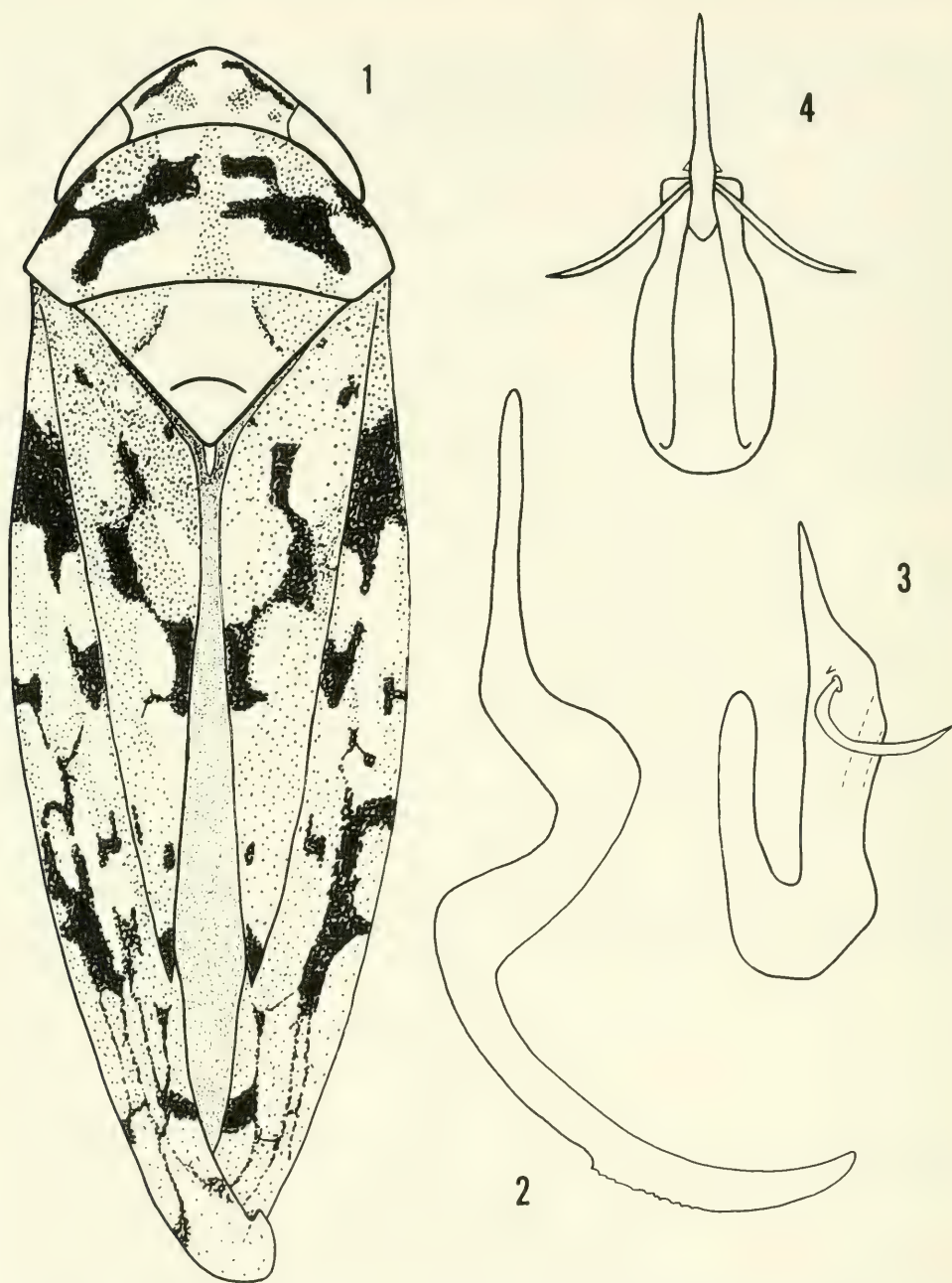
***Xestocephalus bifasciatus* Cwikla and Wolda, NEW SPECIES**

Figs. 5–8

Length.—Male 3.3–3.6 mm, female 3.8 mm.

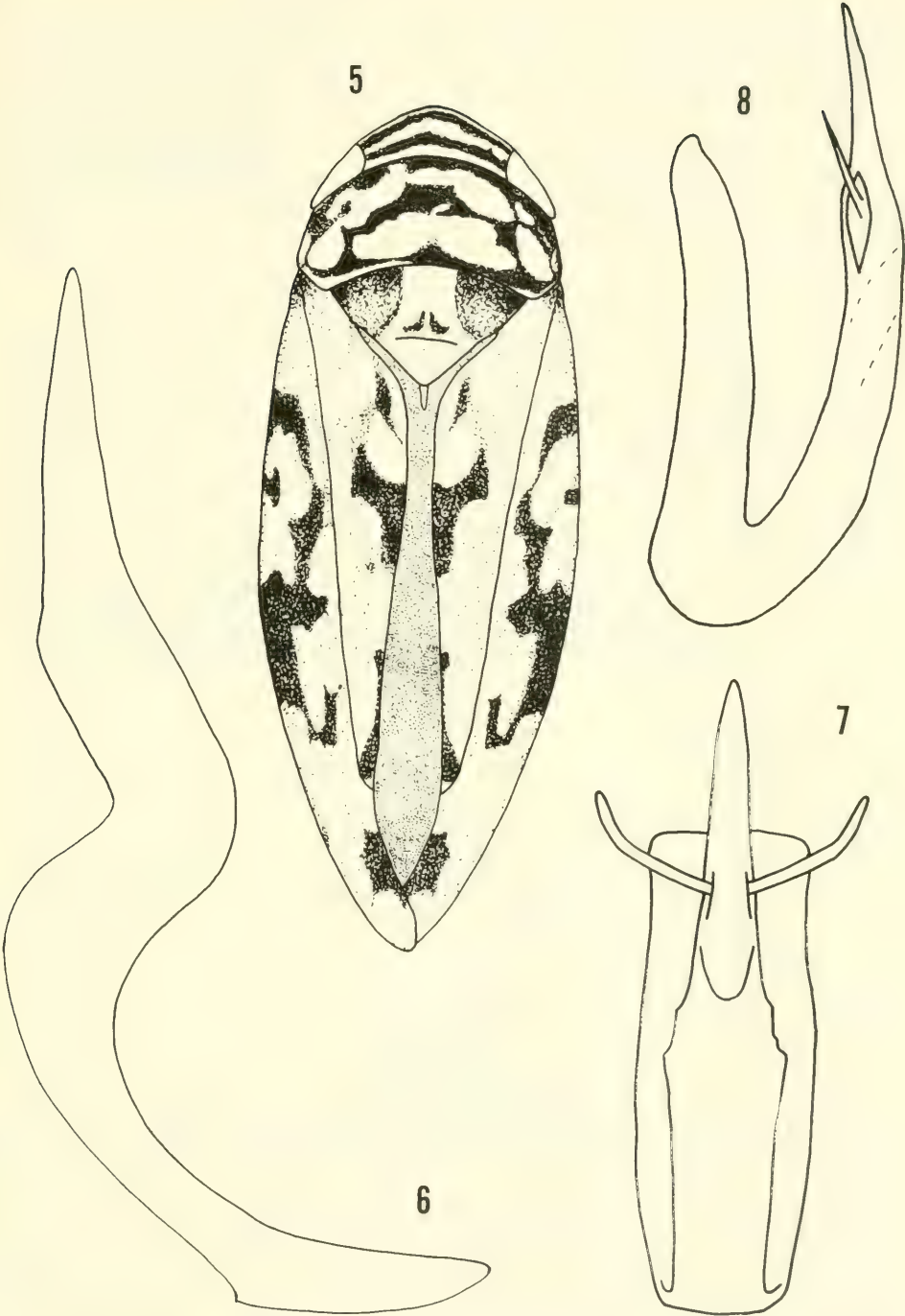
Color.—Crown white with two dark brown transverse bands, bands may be connected by two longitudinal dark brown stripes. Face light brown or white, transverse dark brown band, when present, runs along and connects frontal sutures above antennal pits. Pronotum white and heavily marked with three irregularly shaped bands which connect at lateroposterior margins. Scutellum light brown, anterior margins brown, discal area with brown spot or two brown crescent-like markings. Forewing light brown, irregular dark brown and white markings throughout wing. Lateral aspect of thorax, legs and abdomen light brown.

Male genitalia.—Pygofer with posterior margin produced, internal tooth-like processes directed medially. Plates with apex truncate. Aedeagus in lateral aspect V-shaped, margin of shaft with teeth in posterior aspect, pair of thin processes directed dorsally in posterior aspect, processes appearing to arise from large pit. Gonopore near middle of shaft. Styler apex enlarged, curved.



Figs. 1–4. *Xestocephalus vittanotus*. 1, Habitus, dorsal aspect. 2, Left style, lateral aspect. 3, Aedeagus, left lateral aspect. 4, Aedeagus, posterior aspect.

Type-series.—Holotype ♂ Panama, Chiriquí, Guadalupe Arriba, 2100 meters, 8°52'25"N, 82°33'13"W, 25-IV-1984, H. Wolda coll. Paratypes: one ♂ same data as holotype, one ♀ same data as holotype except for 16–22-V-1984. Holotype and ♀ paratype in DeLong Collection (OSUC) and ♂ paratype in the H. Wolda Collection.



Figs. 5-8. *Xestocephalus bifasciatus*. 5, Habitus, dorsal aspect. 6, Left style, lateral aspect. 7, Aedeagus, posterior aspect. 8, Aedeagus, left lateral aspect.

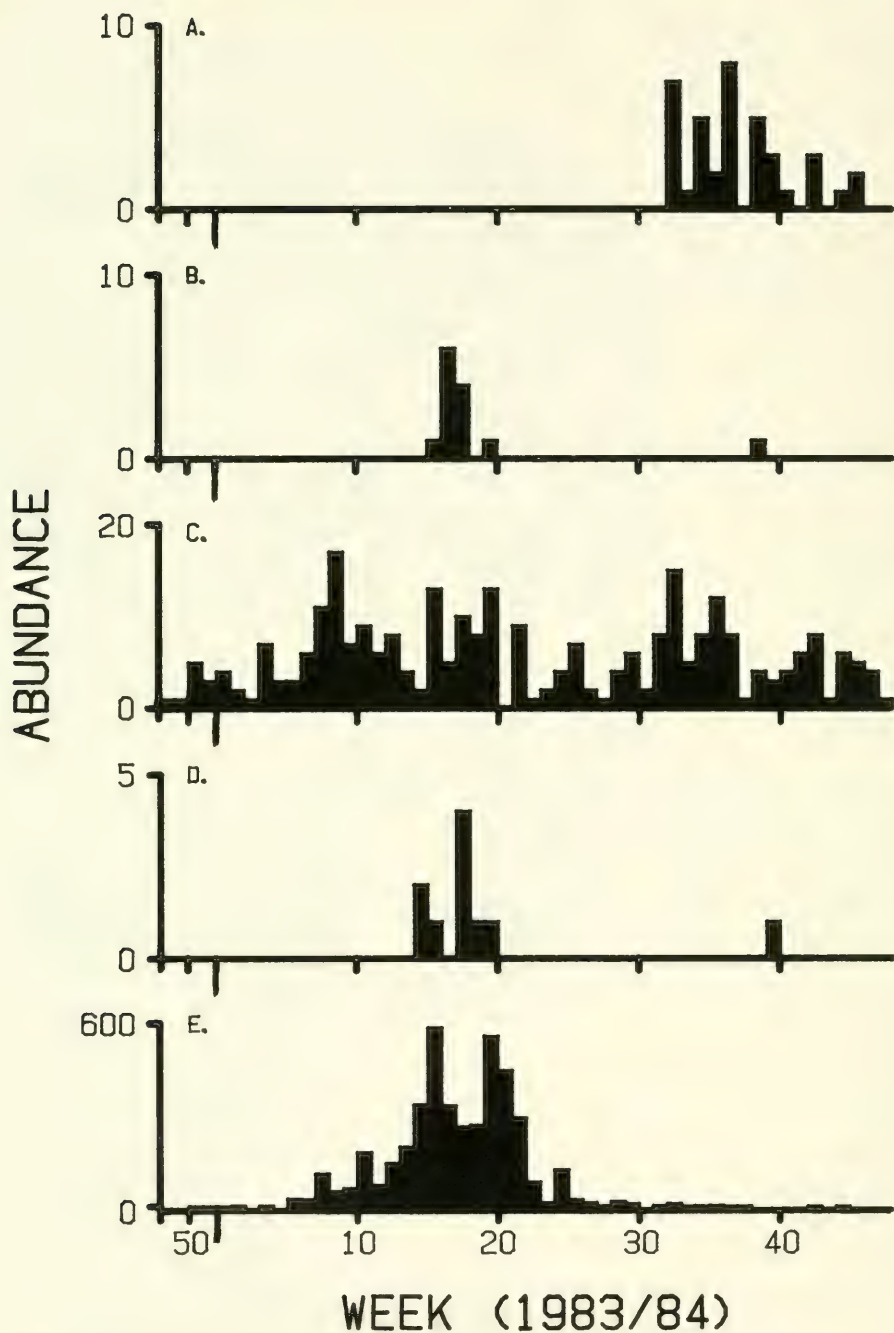


Fig. 9. Temporal abundance for five species of *Xestocephalus* in a light trap at Guadalupe Arriba (Chiriquí, Republic of Panama) from December 1983 through November 1984. The numbers of individuals per week of A) *X. artarus* DeLong, Wolda and Estribi; B) *X. bifasciatus* n. sp.; C) *X. vittanotus* n. sp.; D) *X. desertorum* (Berg); E) *X. fuscus* DeLong, Wolda and Estribi.

Variation.—Minor variation was noted between the members of the type-series in the width of the transverse bands on the crown and pronotum and the presence or absence of two longitudinal brown bands connecting the transverse bands.

Etymology.—Latin, *bi* (two) and *fasciatus* (banded) refer to the two bands on the crown.

Diagnostic features.—This species is related to *fuscarius* DeLong, Wolda and Estribí and can be separated from it and other *Xestocephalus* species by the two dark brown bands on the crown, the thin aedeagal processes in lateral aspect and the teeth on the aedeagal shaft in posterior aspect.

DISTRIBUTION OF THE NEW SPECIES

The junior author has extensively light trapped throughout western Panama and other Panamanian localities (for map of sites see DeLong et al., 1980). The localities of Boquete (1350 meters) and Fortuna (1050 meters) lie respectively 10 and 30 kilometers to the east of Guadalupe Arriba (2100 meters). All localities are contained within Cordillera Central. Light trapping from these two localities has not yet procured individuals of *X. bifasciatus* n. sp. and *X. vittanotus* n. sp. In addition, extensive light trap collecting at sea level in Miramar, Panama for one year and on other lowland areas of Bocas del Toro Province has not yielded these two new species. This suggests that *X. vittanotus* and *X. bifasciatus* might be restricted to the higher elevations of Cordillera Central.

PHENOLOGY OF *XESTOCEPHALUS* SPECIES AT GUADALUPE ARRIBA

While certain auchenorrhynchous Homoptera are active all year, others appear to have a distinct seasonal distribution (Wolda, 1982). Seasonal species from the tropics have a longer season and their seasonal peaks are usually more spread out than their temperate counterparts (Wolda, 1978b). Wolda (1978a) has hypothesized this seasonal activity is correlated with the start of the wet season and the resulting production of new plant growth. Although light trap data are not an absolute collecting method, they do give a good indication of seasonal abundance for nocturnally active adult insects such as leafhoppers (Wolda, 1978b).

The light trap at Guadalupe Arriba yielded five species of *Xestocephalus* during 1984. Their abundance per week is plotted in Fig. 9. Although only one light trap was in operation over a single season, the data obtained do give a rough indication on probable population trends.

Of the five species collected, *X. vittanotus* n. sp. was the only obvious non-seasonal species. Low numbers of individuals were found almost equally abundant throughout the year (Fig. 9C). *Xestocephalus fuscarius* DeLong, Wolda and Estribí is seasonal with vast numbers being collected from mid-February to early June (Fig. 9E). Only scattered individuals were collected during the remainder of the year.

The three remaining species appear to be seasonal. *Xestocephalus bifasciatus* n. sp. and *X. desertorum* (Berg) both have all but one individual collected at the beginning of the rainy season (Fig. 9B, D). On the other hand, *X. artarus* DeLong, Wolda and Estribí, appears to be seasonal with adult abundance lasting between August through November (Fig. 9A). While the numbers of individuals are low

for some of the seasonal species, further collecting from a number of different light traps at Guadalupe Arriba should help to determine the exact nature of their seasonality.

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A NEW SPECIES OF *PLATAEA* (LEPIDOPTERA: GEOMETRIDAE)
FROM TEXAS

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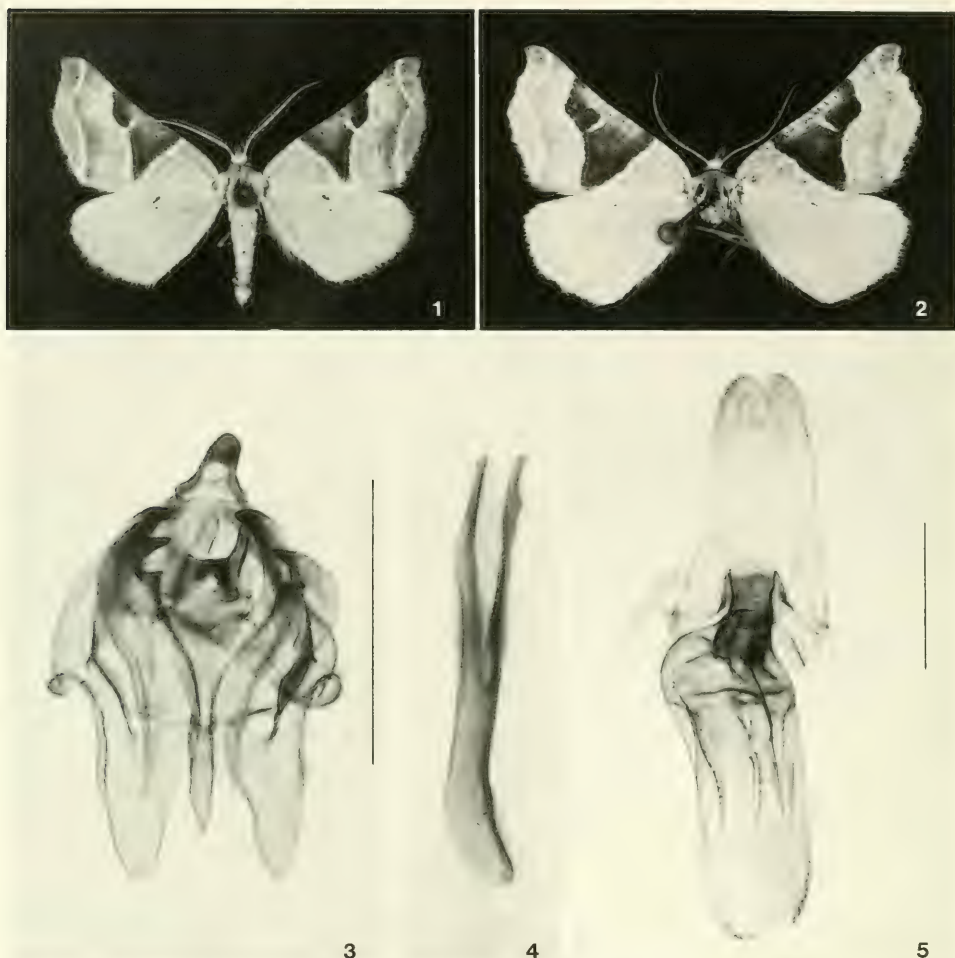
Abstract.—*Plataea blanchardaria* Knudson is described from adults of both sexes collected in Texas. Adults of both sexes and genitalia are figured.

The geometrid genus *Plataea* was revised by Rindge (1976), at which time six species were recognized from western North American and two new species were described from Mexico. The moths are similar in general appearance, being silvery gray or brown, usually with a darker subtriangular median area. As pointed out by Rindge (1976), the male genitalia show an unusual degree of variability between the different species, although other characters are quite uniform. The species described below was collected first by A. & M. E. Blanchard and was assumed to be the same as *P. calcaria* (Pearsall), to which it bears close superficial resemblance. Later, however, when a series of both sexes was obtained, it became obvious that those specimens did not represent *P. calcaria*, which is sexually dimorphic and has very different genitalia.

Plataea blanchardaria E. Knudson, NEW SPECIES

Figs. 1-5

Description.—*Head:* Front and vertex pale ochreous brown (buff colored); front flat, with conical scale tuft extending anteriorly; labial palpi buff colored, porrect, exceeding front by 1 eye diameter. Male antennae bipectinate to apex; pectinations vary from $4\times$ the length of segments near middle to $\frac{1}{2}$ the length of segments at apex; shaft and pectinations buff colored speckled with dark brown. Female antennae shortly bipectinate, terminal 4 or 5 segments serrate. *Thorax:* Buff colored above and below; legs with fuscous irroration on anterior surface of femora and tibiae. Foretibia with epiphysis arising at middle and extending to just beyond tibio-tarsal joint. *Abdomen:* Buff colored above and below. *Forewings:* Sexes alike. Upper surface: Ground color varies from olivaceous white to yellowish white, finely striate with olive brown or orange brown especially along coastal margin. Antemedial line whitish, from costal margin $\frac{1}{3}$ the distance from base, outwardly oblique to just above dorsal margin just beyond middle, from where it joins the postmedial line. Postmedial line whitish, from costal margin at $\frac{1}{3}$ the distance from apex, convex inwardly from lower half of cell to near dorsal margin, where it joins the antemedial line, enclosing the contrastingly darker median area. Median area olivaceous or orange-brown, lighter along costal margin and containing a pale comma-shaped discal spot, which may or may not touch the postmedial line. Subterminal line whitish, produced outwardly at vein M2, margined inwardly



Figs. 1-5. *Plataea blanchardaria*. 1, Holotype male. 2, Female. 3, Male genitalia of paratype (slide ECK 1209), ventral view, aedeagus removed. 4, Aedeagus (slide ECK 1222). 5, Female genitalia of paratype (slide ECK 1220). Figs. 3 and 4 at same magnification. Line segments = 1 mm.

with darker suffusion and outwardly with darker suffusion near apex. Fringe concolorous with ground, checkered with blackish at vein ends. Under surface: pale olivaceous or orange brown, unmarked, except for pale subterminal line near apex. *Hindwings*: Upper surface: Brownish white to pale orange, slightly darker towards termen; thin dark terminal line; fringe whitish. Under surface: Whitish, striated with olivaceous or orange brown, especially along cubital margin. *Length of forewings*: Males: $n = 8$, 11.9-12.4 mm, avg. 12.2 mm. Females: $n = 5$, 13.8-14.6 mm, avg. 14.2 mm. *Male genitalia* (Figs. 3, 4): Uncus well sclerotized, projecting ventrally, broadly rounded dorsally, apex with a single minute ventrally directed point; gnathos well sclerotized, U-shaped, with elongate, undivided median process. Valvae complex, heavily sclerotized, and broadly fused to saccus and juxta; saccus with two broad, inwardly curving processes posteriorly; costa produced anteriorly into a sclerotized rod, posteriorly, with apex an inwardly

directed blunt point, giving each valve a three-lobed appearance. Saccus invaginate medially with broad rounded lateral lobes; juxta Y-shaped, with elongate anterior median process. *Male genitalia*: Aedeagus well sclerotized, bifid posteriorly for half its total length, vesica membranous. Eighth abdominal segment simple, unmodified. *Female genitalia* (Fig. 5): Papillae anales broad, membranous, with numerous short setae; apophyses posteriores $3\times$ the length of apophyses anteriores; sterigma a short sclerotized tube with lamina antevaginalis well sclerotized laterally; ductus bursae short, well sclerotized, with 3–4 longitudinal ridges; corpus bursae elongate, posterior $\frac{2}{3}$ sclerotized, with 7–8 serrate longitudinal ridges, anterior $\frac{1}{3}$ membranous.

Types.—Holotype (Fig. 1): ♂ 8 mi W of Premont, Duval Co., Texas, 30-VI-85, collected by J. E. Gillaspay, and deposited in the National Museum of Natural History, Washington, D.C. (NMNH). Paratypes: 4 mi NE of Jct. FM 1329/2295, Duval Co., Texas, 27-V-85, 6 ♂, 1 ♀, collected by J. E. Gillaspay, 1 ♂ in American Museum of Natural History, New York, N.Y. (AMNH), 1 ♂ retained by author, others by collector; Mitchell Ranch, Live Oak Co., Texas, 30-XI-85, 1 ♂, collected by Pam H. Prewitt, in Texas A&I University collection: U.S. 90 at Nueces River (8 miles west of Uvalde), Uvalde Co., Texas, 12-IX-71, 1 ♂, collected by A. & M. E. Blanchard, in NMNH; Seminole Canyon State Park, Val Verde Co., Texas, 23-V-81, 5 ♀, collected by E. C. Knudson, 1 in NMNH (Fig. 2), 1 in AMNH, 3 retained by author.

Remarks.—*Plataea blanchardaria* is superficially similar to *P. calcaria*, although females of *calcaria* do not have dark suffusion in the median area of the forewing. The genitalia of both sexes are very different from all other *Plataea* species but with similarities to *P. calcaria*. Male *calcaria* have a single, inwardly directed process of the sacculus and a similar though reduced juxta, differing most markedly in the much longer costal portion of the valve and the much smaller saccus. Female genitalia of both species are similar, but those of *calcaria* lack the sclerotized serrate ridges in the corpus bursae. This new species is named to honor André Blanchard in gratitude for the immeasurable assistance and inspiration that he has given me.

ACKNOWLEDGMENTS

The author is very grateful to James E. Gillaspay for the loan (and gift) of specimens and to the National Museum of Natural History for loan of specimens. I am also very grateful to Douglas C. Ferguson and Frederick H. Rindge for reviewing the manuscript and providing helpful suggestions. I thank the Texas Parks and Wildlife Department for providing access to collecting some of the type series. Finally, I thank André Blanchard for assistance in preparing the photographic plates.

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A NEW SPECIES OF *LINOGNATHOIDES*
(POLYPLACIDAE: ANOPLURA) FROM BLACK-TAILED PRAIRIE DOG,
CYNOMYS LUDOVICIANUS (ORD) (SCIURIDAE: RODENTIA)

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Abstract. — *Linognathoides cynomyis* (Polyplacidae: Anoplura), new species, is described from the black-tailed prairie dog, *Cynomys ludovicianus* (Ord), in South Dakota. Adults and three nymphal stages of this species are illustrated and relationships to allied species, *L. laeviusculus* (Grube) and *L. marmotae* (Ferris), are discussed.

Linognathoides species are known from holarctic Marmotini (northern ground squirrels) and Afrotropical Xerini (African ground squirrels). *Linognathoides laeviusculus* (Grube), a polytypic species, is commonly found on many species of *Spermophilus*, whereas *L. marmotae* (Ferris) is a parasite of the North American marmots, *Marmota*. *Cynomys ludovicianus* (Ord), the black-tailed prairie dog, had been reported to harbor *L. marmotae* (Ferris, 1951; Kim and Adler, 1982).

For the first time, large and comprehensive collections of a *Linognathoides* species from *C. ludovicianus* in South Dakota were made by Mr. Glenn E. Kietzmann, Department of Zoology, Iowa State University. This taxon is distinctly different from *L. marmotae* and *L. laeviusculus* and is described as a new species here. Morphological terminology of Kim and Ludwig (1978) is followed for description in this paper.

Linognathoides cynomyis Kim, NEW SPECIES

Neohaematopinus marmotae Ferris (*partim*): Ferris 1951, Mem. Pac. Coast Entomol. Soc. 1: 293 (records from *Cynomys ludovicianus*).

Linognathoides marmotae (*partim*): Kim and Adler, 1982, J. Med. Entomol. 19: 621 (records from *Cynomys ludovicianus*).

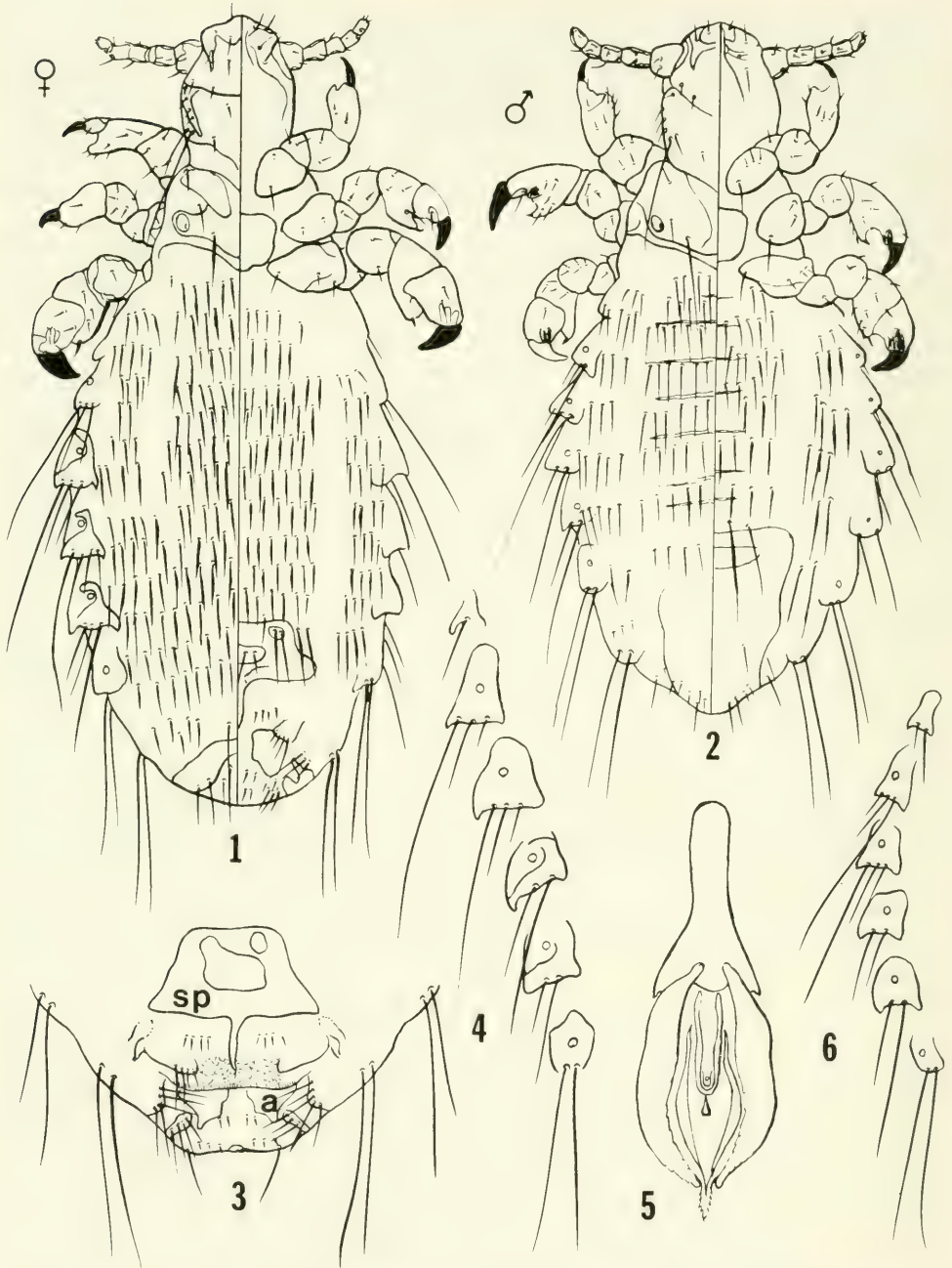
Type data.—♂ holotype, ♀ allotype, 12 ♂, 18 ♀, 14 third-stage nymph, 10 second-stage nymph, and 1 first-stage nymph paratypes from *Cynomys ludovicianus* ♂, Pennington County, Box Elder, South Dakota, June 1983, G. E. Kietzmann. Other paratypes were collected from the same host (10 animals) by G. E. Kietzmann at the same location in 1982: 6 ♂, 26 ♀, 5 third-stage and 2 second-stage nymphs, June 20; 16 ♂, 13 ♀, 6 third-stage, 6 second-stage and 1 first-stage nymphs, June 18; 6 ♂, 34 ♀, and 1 third-stage nymph, June 25; 4 ♂, 1 ♀, 1 second-stage and 1 first-stage nymphs, June 27; 2 ♀, July 24; 2 ♀ and 1 third-stage nymph, August 6. Holotype, allotype, and paratypes are deposited in the collection of The Frost

Entomological Museum, The Pennsylvania State University, and a series of paratypes are in the collection of Glenn E. Kietzmann.

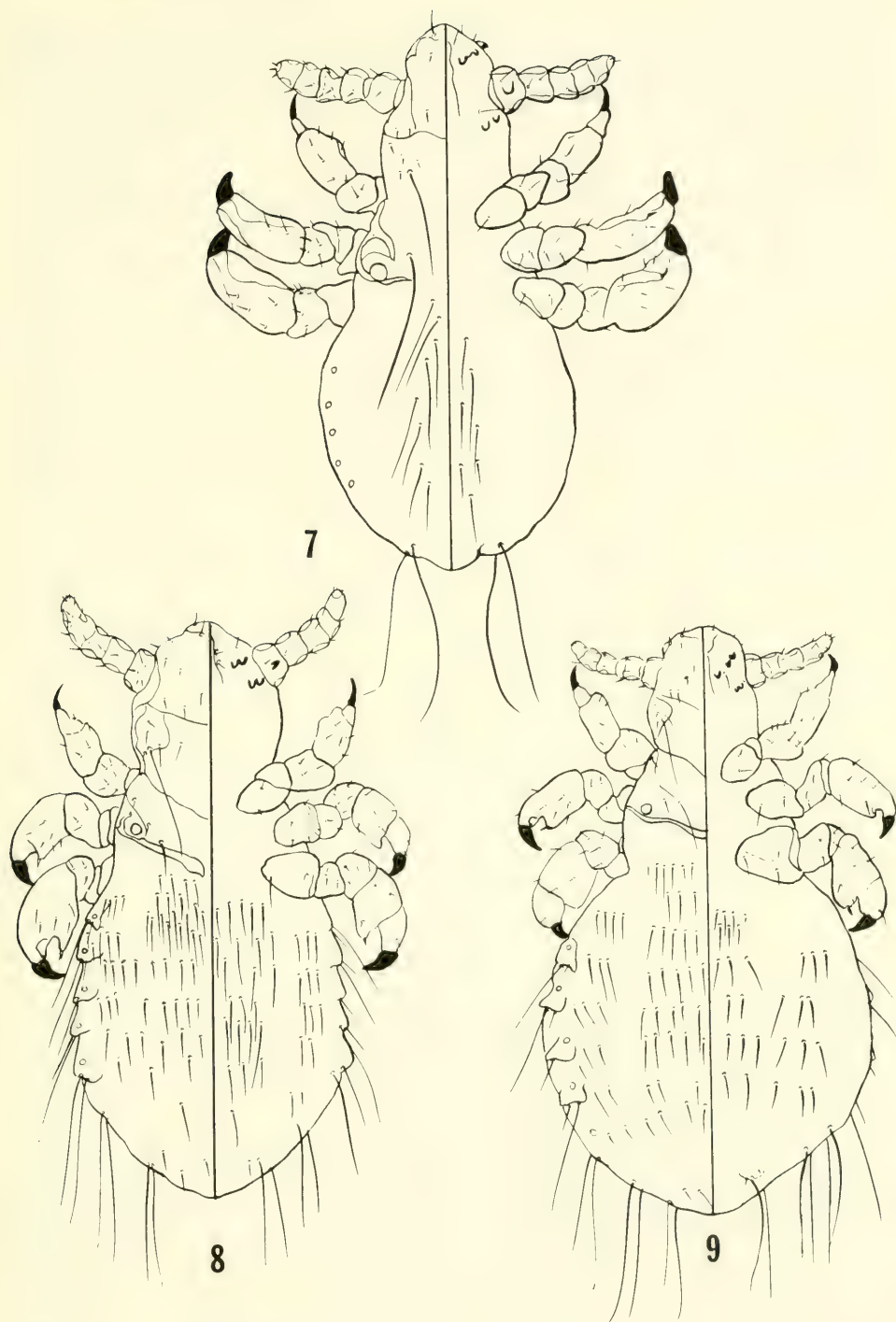
Diagnosis.—Closely related to *Linognathoides marmotae* and *L. laeviusculus*. Males of *L. cynomyis* differ from those of two most similar species by having the thoracic sternal plate rounded posteriorly (Figs. 13–15), and females are separable from other species by the thoracic sternal plate posteriorly emarginate with its middle apex slightly convex (Figs. 10–12), and mesothoracic spiracles (0.33 mm in diameter) smaller than those of *L. marmotae* but much larger than those of *L. laeviusculus*. The first-stage nymph of *L. cynomyis* differs from those of its most similar species by having long DPHS (dorsal principal head setae) passing far beyond DPTS (dorsal principal thoracic setae) and almost reaching posterior end of thorax, long DPTS reaching 3rd and 4th abdominal spiracles, and long DCAS (dorsal central abdominal setae). The second- and third-stage nymphs of this new species differ from those of *L. marmotae* and *L. laeviusculus* by having 7–8 CAS (central abdominal setae) on each of the abdominal segments 4 to 7, and 3 LAS (lateral abdominal setae) on each side of the segments 4 to 6.

Description.—Total body lengths: Male holotype 1.45 mm, female allotype 2.00 mm; male 1.42 mm ($\bar{x}$) ($n = 5$, range 1.38–1.47 mm); female 1.97 mm ($\bar{x}$) ($n = 6$, range 1.86–2.08 mm); third-stage nymph 1.32 mm ($\bar{x}$) ($n = 11$, range 1.25–1.50 mm); second-stage nymph 1.02 mm ($\bar{x}$) ($n = 12$, range 0.90–1.14 mm); first-stage nymph 0.79 mm ($\bar{x}$) ($n = 2$, range 0.69–0.90 mm).

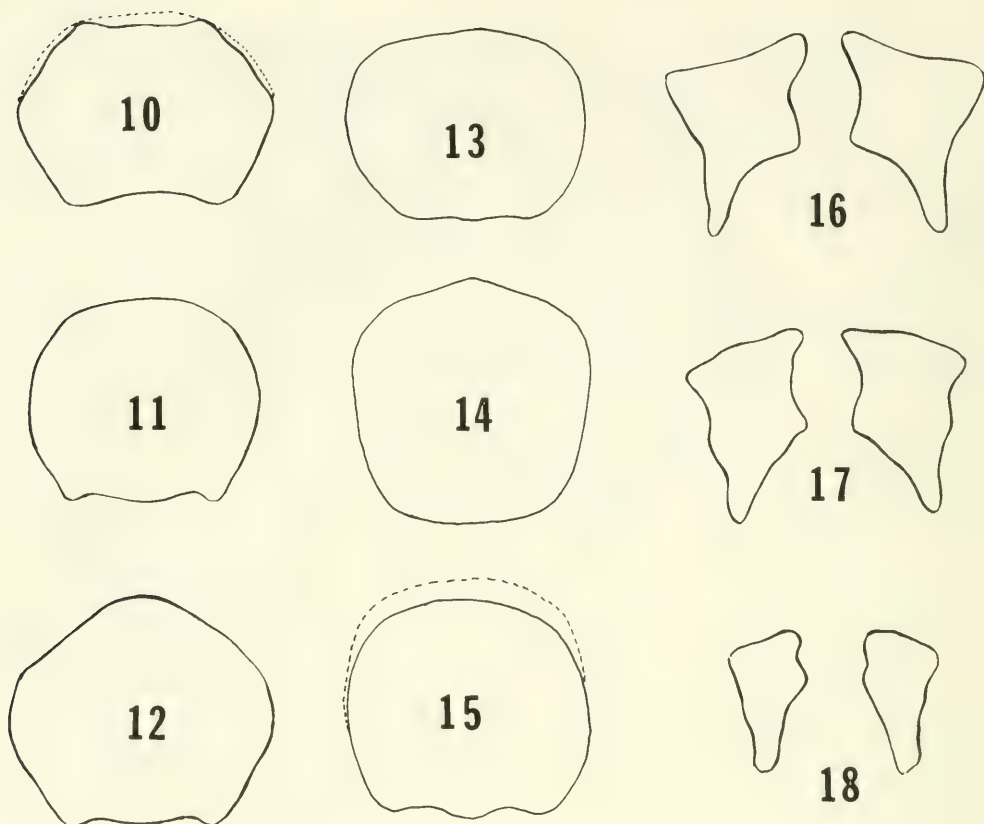
Male (Figs. 2, 5, 6, 14).—Head and thorax well sclerotized but abdomen weakly sclerotized. *Head* slightly longer than wide, anterior apex broadly rounded; 2 SHS (sutural head setae) and 4 DMHS (dorsal marginal head setae) distinct on each side; DPHS long, passing beyond thoracic spiracle; DAChS (dorsal accessory head setae) longer than DMHS (dorsal marginal head setae); DPoCHS (dorsal posterior central head setae) and VPHS (ventral principal head setae) distinct; antennae 5-segmented, without sexual dimorphism, with the basal segment larger than the second segment, slightly wider than or as wide as long. *Thorax* broader than long; thoracic sternal plate (Fig. 14) with anterior apex slightly angularly rounded and posterior apex evenly rounded; mesothoracic spiracle (0.033 mm in diameter) moderate in size; DPTS (0.139 mm) long, reaching the second abdominal tergite; DPtS (dorsal prothoracic setae) and DMsS (dorsal mesothoracic setae) distinct. *Legs* with subtriangular coxae; forelegs small, each with acuminate claw; hindlegs much larger than midlegs, each with strong, pointed tarsal claw. *Abdomen* wider than thorax, poorly sclerotized, with one thin plate per segment dorsally and ventrally; 8 rows of DCAS, each with 8–11 setae; 7 rows of DLAS (dorsal lateral abdominal setae), each with 2–4 setae; abdominal sternites weaker, narrower than tergites, one or two rows of VCAS (ventral central abdominal setae), each row with 6–10 setae, segment 1 with 2 setae on each side, and 8th row with 4 setae; 5 rows of VLAS (ventral lateral abdominal setae) present, each with 4–5 setae. Paratergites (Fig. 6) present on segments 2 to 7: plate I with one short and one long apical setae; plates II and III each with one long, one intermediate, and one short setae; plates IV and V each with dorsal seta long and ventral seta shorter; plate VI with 2 long setae; dorsal angles of paratergites II–IV slightly produced into points; paratergites II–VI each with spiracles. *Genitalia* (Fig. 5) with distinct subgenital plate; basal apodeme narrow anteriorly; parameres apically narrow;



Figs. 1-6. *Linognathoides cynomyis* Kim, n. sp. 1, Female. 2, Male. 3, Female genitalia: a, adgenital plate; sp, subgenital plate. 4, Female paratergites. 5, Male genitalia. 6, Male paratergites.



Figs. 7-9. *Linognathoides cynomyis* Kim, new species. 7, First-stage nymph. 8, Second-stage nymph. 9, Third-stage nymph.



Figs. 10-15. Thoracic sternal plates. 10-12, Females. 13-15, Males. 10, *Linognathoides laevisculus* (Grube). 11, *L. cynomyis* Kim, n. sp. 12, *L. marmotae* (Ferris). 13, *L. laevisculus* (Grube). 14, *L. cynomyis* Kim, n. sp. 15, *L. marmotae* (Ferris). Figs. 16-18. Female adgenital plate. 16, *L. marmotae* (Ferris). 17, *L. cynomyis* Kim, n. sp. 18, *L. laevisculus* (Grube).

pseudopenis long, narrow, serrated laterally, extending well beyond apices of parameres.

Female (Figs. 1, 3, 4, 11, 17).—Head, thorax, and legs as in male unless described otherwise. DAChS and DMsS long; thoracic sternal plate (Fig. 11) anteriorly evenly rounded and posteriorly emarginate, with its middle apex slightly convex. *Abdomen* weakly sclerotized, without distinct dorsal and ventral plates except those of genitalia, with numerous setae; 13 rows of regular setae, each with 10-12 CAS and 3-4 LAS on each side; paratergites I-IV subtriangular, and V-VI subrectangular. *Genitalia* (Figs. 3, 17) with subgenital plate trapezoid, middle apex narrowly extended; gonopods VIII small, with 3-4 setae; gonopods IX with 4-5 long setae; adgenital plate slightly longer than wide (Fig. 17).

Third-stage nymph (Fig. 9).—*Head* with 10 ventral tubercles, two paired tubercles placed at the base of first antennal segment; SHS, DMHS and DAChS distinct; DPHS long, reaching mesothoracic spiracles; DPHS and DAChS placed on lateral convexity; VPHS long, reaching the middle part of first antennal segment. *Thorax* without sternal plate; DPtS and DMsS distinct; DPtS short, barely reaching first row of DCAS. *Legs* similar to those of adults. *Abdomen* membra-

nous, with 5 distinct paratergites on each side; 8 rows of DCAS, each with 6–10 setae; 6 rows of DLAS, each with 2–4 setae on each side. Paratergites present on segments 3 to 6, each with one short and one long apical setae.

Second-stage nymph (Fig. 8).—Similar to third-stage nymph. *Head* with 2 paired ventral tubercles placed next to first antennal segment; first antennal segment with ventral tubercle.

First-stage nymph (Fig. 7).—*Head* with 4 ventral tubercles, paired tubercles placed posterior to first antennal segment which bears a ventral tubercle; SHS, DMHS and DAcHS small; DPHS long, reaching beyond mesothoracic spiracle; VPHS long. *Thorax* with large mesothoracic spiracle, with DPTS long, reaching the middle of abdomen; DPtS distinct but DMsS minute or lacking; no sternal plate present. *Abdomen* without paratergites; 5 spiracles present on each side, 8 DCAS, and 7 VCAS; paired MAS (marginal abdominal setae) long.

Discussion.—*L. cynomyis* new species is most similar to *L. marmotae* and perhaps *L. laeviusculus*. The first-stage nymphs of all three species are very much alike, although there are minor differences, such as the location and number of head ventral tubercles and size of DPHS and DPTS. The second- and third-stage nymphs of *L. cynomyis* are distinctly different from *L. marmotae* and *L. laeviusculus*, having more abdominal setae, such as DCAS, DLAS, and paired ventral tubercles at the base of the first antennal segment; these characters are similar to those found in *L. pectinifer* (Neumann) which is parasitic on the African *Atlantoxerus gotulus*, while the nymphs of *L. marmotae* and *L. laeviusculus* are more similar to each other.

Many characters of *L. cynomyis* adults such as the thoracic sternal plate and adgenital plate are intermediate between *L. marmotae* and *L. laeviusculus*. The thoracic sternal plate of *L. cynomyis* for both male and female represents an intermediate type (Figs. 10–15). Similarly, the adgenital plates of *L. marmotae* are subtrapezoid and of *L. laeviusculus* are oblong-triangular, whereas those of *L. cynomyis* are slightly elongated subtrapezoid (Figs. 16–18). The mesothoracic spiracles of *L. marmotae* females are large, 0.056 mm ($\bar{x}$) in diameter, whereas those of *L. cynomyis* are 0.033 mm in diameter; the spiracles of *L. laeviusculus* females are smallest with 0.013 ($\bar{x}$) mm in diameter.

ACKNOWLEDGMENTS

This new species would not have been discovered for a long time without the efforts of Glenn E. Kietzmann. I thank Mr. Kietzmann for his efforts in collecting and making the materials available to me for study. I am also grateful to April Mercur and Chester J. Stojanovich for their help with the illustrations and to K. C. Emerson, C. W. Pitts, J. R. Stauffer, S. R. Jones, and Glenn E. Kietzmann, and S. Tessler for reading the manuscript. This article was authorized on Jan. 14, 1986 for publication as paper no. 7330 in the Journal Series of the Pennsylvania Agricultural Experiment Station and is a contribution from The Frost Entomological Museum (AES Proj. no. 2594).

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ABSTRACTS FROM A SYMPOSIUM: INSECT-CAUSED GALLS

Foreword

Following are six extended abstracts of papers presented on December 11, 1985 in a symposium entitled "Insect-Caused Galls." The symposium was sponsored by Section C (Ecology, Behavior and Bionomics) of the Entomological Society of America and was held in conjunction with the Society's national conference in Hollywood, Florida. This was the first symposium devoted to discussion of galls ever held at an ESA national conference.

Many entomologists, botanists and ecologists are either directly or indirectly involved with studies of herbivorous insects. For many years considerable attention has been focused on interactions between insects and plants and on the insects' impact on plants. With plant galls we have examples of extremely finely tuned, intimate insect/plant interactions. The plant under the direction of an insect forms an often structurally complex domicile for the insect and in many cases also provides the insect with an enriched diet. Our understanding of herbivorous insects, trophic relationships, micro-community structure, plant defense, and evolution have all benefitted from detailed studies of galls.

Topics for discussion at the symposium were chosen so as to highlight areas of gall research that have provided and will continue to provide useful and intriguing biological information. As with the symposium, we hope that the following papers will bolster, revive, or create an interest in galls among readers.

I acknowledge the enthusiastic participation of my five fellow contributors to the symposium. I thank also the Publications Committee of the Entomological Society of Washington for assistance in producing these symposium proceedings.

Hiram G. Larew, *Symposium Organizer, Florist and Nursery Crops Laboratory, Agricultural Research Service, USDA, Building 470, BARC-East, Beltsville, Maryland 20705.*

HYPOTHESES ON THE ADAPTIVE NATURE OF GALLS

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Abstract.—Hypotheses on the adaptive nature of galls are reviewed. The Non-adaptive, Plant Protection, Mutual Benefit, Nutrition, Microenvironment, and Enemy Hypotheses are evaluated and the last three are supported. Questions in need of study are suggested for each of the viable hypotheses.

The adaptive significance of insect galls has been discussed in the literature many times, but little emphasis has been placed on testing hypotheses. To foster such activity we review the ideas generated in the literature and suggest studies needed to evaluate the hypotheses.

Bequaert (1924) regarded gall characters as having no selective value—*The Nonadaptive Hypothesis*. He noted that nectaries on galls performed no important function. However, Washburn (1984) showed that nectaries on galls attract ants that suppress parasitism on the galler from 48% in their absence to 25% in their presence. Other adaptive features, discussed later, include increased nutritional quality of the gall and reduced chemical defenses. There seems to be no support for this hypothesis and it will not be considered further.

Mani (1964) has argued that galls are a form of plant defense by which the plant encapsulates a herbivore—*The Plant Protection Hypothesis*. However, galls reduce growth and reproduction of plants (e.g. Craig et al., 1986). Also, if galling capability is a plant defensive trait we should see galling strongly linked to plant phylogenies, as are chemical defenses such as mustard oils, cardiac glycosides and alkaloids. In fact analysis of lists in Felt (1940) clearly indicate that phylogenetic links are much stronger with the galling taxa than with the plant taxa. The first line of plant defense against a galler seems to be resistance to gall formation (e.g. Whitham, 1980). Therefore, we do not regard this as a viable hypothesis.

Cockerell (1890) suggested that galls act as protection for the plant and abundant food for the galler—*The Mutual Benefit Hypothesis*. However, gallers reduce plant reproduction (except fig wasps), and must be regarded as parasites (Weis and Kapelinski, 1984). No increased fitness in galled plants has ever been demonstrated (except the figs), so the hypothesis must be rejected.

Many authors have noted higher concentrations of potentially nutritive compounds in galls, such as nitrogen, protein, phosphate, and lipids (e.g. Shannon and Brewer, 1980), as well as reduced defensive chemicals (e.g. Meyer, 1957)—*The Nutrition Hypothesis*. In our own studies on *Euura lasiolepis* Smith, total protein is higher, and total phenols are much lower in gall tissue than in equivalent

tissue in ungalled shoots. A weakness in this hypothesis is that nutritional requirements of gallers are largely unknown. Therefore, two questions that need to be studied are: 1. Do increased "nutrients" in the gall really improve nutritional quality for gallers?; and 2. Do reduced defenses improve survival of gallers? At present there is support for the nutrition hypothesis, but it is correlational in nature, not mechanistic.

Felt (1940) took it for granted that galls provide food and protection for the galler, with emphasis on "shelter from the elements." Which physical factors are of importance is debatable. Plant tissue follows ambient temperatures closely, so insulation is unimportant, as confirmed for gallers by Uhler (1951) and Baust et al. (1979). Hygrothermal stress seems to be a more likely selective force in this *Microenvironment Hypothesis*. On an altitudinal gradient from the San Francisco Peaks down into the Sonoran Desert in Arizona, Wilson Fernandes has documented a significant increase in the number of galling species in the drier environments at lower elevations. Such a pattern is not seen in riparian habitats on the altitudinal gradient, indicating that altitude is less important than dryness of the habitat. Therefore, the microenvironment hypothesis is supported, although again the evidence involves correlation. Answers to the following questions would help in testing this hypothesis: 1. What are the benefits of transitional stages between free leaf feeders and gallers (e.g. leaf folders)? 2. What are the global geographic distributions of galling species richness?

Many authors have noted the protective nature of galls against natural enemies, particularly parasitoids. Larger galls reduce parasitoid attack (e.g. Weis et al., 1985), and diversity of gall types in a community has been accounted for by selection for divergence by parasitoids (e.g. Askew, 1961; Cornell, 1983)—*The Enemy Hypothesis*. One problem with the hypothesis is that gallers without parasitoids seem to show divergence of gall types as well developed as those with parasitoids (e.g. eriophyid mites, *Pemphigus* aphids, and *Adelges* galls without parasitoids, compared to cynipid, cecidomyiid and tenthredinid galls with parasitoids). Another problem is that divergence in gall morphology frequently does not reduce access to parasitoids, as in *Neuroterus* spangle galls on oak leaves (cf. Darlington, 1975). Also, larger *Pontania* galls are more heavily parasitized than smaller galls in the Flagstaff area (Karen M. Clancy, personal communication), so large gall size is not always associated with better protection. Finally, an alternative hypothesis seems to be equally viable: genetic drift results in divergence of gall morphology because there is no stabilizing selection keeping galls of reproductively isolated species the same in morphology. Thus, two questions need to be addressed: 1. Does character displacement occur in gall morphology? 2. Do galling species with parasitoids show more gall divergence than those without parasitoids? Since gall size provides protection against parasitoids in some cases, there is some support for this hypothesis. However, more studies are needed before its validity is adequately tested.

During the evolution of the galling habit two pathways have been followed, one via plant mining and boring (e.g. tephritid and agromyzid flies, and Lepidoptera), and the other via sedentary feeding, and production of differential plant growth (e.g. aphids, psyllids, thrips, mites, and cecidomyiids). The selective advantages involved with galling will be slightly different in each case. Plant miners are already protected from hygrothermal stress, so initiation of swelling in plant tissue during

gall formation would provide improved food supply and protection from enemies. Sedentary surface feeders which cause differential plant growth to form feeding depressions would benefit mainly from a more protected microenvironment, since nutrition and protection from enemies need not change. The further development of feeding depressions into closed galls would be favored by selection for improved microenvironment and nutrition, and reduced enemy attack.

Although the Nutrition, Microenvironment, and Enemy Hypotheses seem to be the most viable of the six discussed, none has been adequately tested and various problems need resolution. However, we hope that this discussion will revive the old debate on the adaptive nature of galls (e.g. Romanes, 1889; Wetterhan, 1889), and stimulate more detailed tests among hypotheses.

ACKNOWLEDGMENTS

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THE IMPACTS OF GALLS AND GALLMAKERS ON PLANTS

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Abstract.—Gallmakers may have a number of negative impacts on host plants. In this paper, we report several negative effects of the tephritid *Eurosta solidaginis* (Fitch) on the composite *Solidago altissima* L. This gallmaker's impacts are appreciable on ramets (individual shoots) and include decreased leaf and inflorescence allocation, reduced rhizome numbers, redirection of host resources to the gall, and the loss of rhizome connections between galled ramets and the remainder of the clone. Because of localization of the gallmaker's impact and the clonal nature of the host plant, gallmaker impacts are negligible in mature clones. However, gallmaker attack on an establishing clone can reduce the lifetime fitness of its host. The results for this one gallmaker can not be generalized to other gallmakers, as the effects of each gallmaker will vary depending upon gallmaker seasonal cycles, host clonality, organs attacked, tissues stimulated, reactions, and the degree of resources mobilized. By detailing gallmaker impacts, we will gain insights into the selection pressures, evolutionary responses, and degree of reciprocal adaptation in plant-gallmaker interactions.

Herbivory by gallmakers has the potential to result in a number of negative impacts on host plants. This paper is an attempt to detail some of those negative effects. However, because it is premature to make generalizations about the impacts of all gallmakers, we will detail one gallmaker's impact with the hope of stimulating additional studies.

Gallmakers, unique among herbivores, alter the development of plant tissues to form a tumor-like growth from which the gallmaker gains both nutrition and protection (Abrahamson and Weis, in press). It is likely, then, that the impacts of gallmakers are more severe than those of other herbivores when measured on a per herbivore basis. Further, it is important for us to view the gall phenotype as a result of the interactions between two genotypes: the gallmaker's, coding for the stimulus, and the plant's, for the reaction. It follows that the evolution of these two genotypes could be intimately tied to one another.

Gallmakers, as plant parasites, should evolve the means to manipulate their hosts so as to balance immediate gains with the future availability of suitable hosts. This could mean in some gallmaker-host systems that the gallmaker will evolve to minimize its impact on its host plant. Likewise, host plants, if sufficiently damaged by gallmakers (and other herbivores), should also evolve characteristics to reduce these impacts. This might include the elaboration of chemical defenses

or a reduction in reactivity to the gallmaker. These evolutionary possibilities suggest the importance of examining gallmaker impacts in light of unilateral versus reciprocal adaptation. Gallmaker-host plant interactions form one of the better systems to critically evaluate the "co-" in coevolution.

The negative impacts of gallmakers infesting certain agricultural crops are well documented (e.g. grape phylloxera, Hessian fly; Riley and Howard, 1891; McCulloch, 1923). But, the frequency and degree to which gallmakers injure their hosts in natural situations is still open to question. Some workers have suggested that gallmaker impact is negligible (Wangberg, 1978; Gandar, 1979), however, quantitative analyses have repeatedly shown that galls are metabolic sinks for carbon (Fourcroy and Braun, 1967; Jankiewicz et al., 1970; Hartnett and Abrahamson, 1979; Weis and Kapelinski, 1984; McCrea et al., 1985), energy (Stinner and Abrahamson, 1979), and some mineral elements (Palci and Hassler, 1967; Abrahamson and McCrea, 1986). Obviously, when reproductive tissues are affected by gallmakers, the potential for negative impact is high (Harris, 1980; Collins et al., 1983). It is clear that as gallmakers procure their nutritional requirements they not only "rob" the host plant of the consumed tissue, but they also cause the plant to alter tissue that would otherwise serve productive functions in plant growth and reproduction (Abrahamson and Weis, in press).

Unfortunately, few gallmakers have been examined from the perspective of the impacts on their hosts. We do, however, have a growing body of data for one stem gallmaker, the tephritid *Eurosta solidaginis* (Fitch). This *Eurosta* attacks a hexaploid composite, *Solidago altissima* L. (tall goldenrod), and directs the formation of the goldenrod ball gall. Because this host is a rhizomatous, long-lived perennial, we must examine gallmaker impacts at two levels: the individual shoot (ramet) level and the genetic individual (genet) level. It is the latter level that is most crucial to understanding the potential for plant evolutionary responses to the gallmaker. In addition, we must use several currencies to measure these impacts since gallmakers use proteins for structural building blocks while their hosts use carbohydrates (Abrahamson and McCrea, 1986).

We have determined ball gallmaker impacts are appreciable at the ramet level in each of several currencies. An energy flow model, using ramet production, gall growth, and gallmaker growth, respiration, and egestion, showed that approximately 7% of the ramet's energy goes to support the ball gall and gallmaker (Stinner and Abrahamson, 1979). We have also found appreciable concentration of mineral elements (e.g., N and P) by two gallmakers that attack goldenrod. The ball gall and its gallmaker, for example, account for approximately 3.5% of a ramet's N (Abrahamson and McCrea, 1986). In another study examining biomass allocation as influenced by ball gallmakers, it was found that gallmakers decreased leaf and inflorescence allocation and reduced new rhizome numbers and biomass (Hartnett and Abrahamson, 1979). This latter finding is especially intriguing as it suggests the possibility of a carry-over of a gallmaker's impact into a subsequent season. To examine this, we induced galls in small two-ramet clones during the 1984 growing season. After overwintering, these clones were grown in the absence of gallmakers. Clones with 1 or 2 galls in 1984 had significantly fewer ramets in 1985 than the ungalled control clones (McCrea and Abrahamson, unpublished data). Thus, genets which lose resources to this gallmaker during their first year or two could potentially suffer fitness losses over their lifetime.

In an attempt to clarify the ball gallmaker's impact on biomass allocation and photoassimilate translocation, we used ^{14}C labeled CO_2 introduced to individual leaves above and below galls of different sizes. We learned that large galls intercepted a significant portion of the photoassimilate moving through the stem, but that the gall did not mobilize photoassimilates towards it (McCrea et al., 1985). In a similar experiment that used two-ramet clones, we found that while defoliation of the ramet opposite the labeled ramet induced translocation of photoassimilates to the defoliated ramet, ball gall presence did not. Thus, the gallmaker's impact was localized, possibly as a result of either the gallmaker acting as a "good" parasite and/or the host's reaction (McCrea and Abrahamson, unpublished data).

In another experiment, we created three ramet clones and induced zero to three galls/clone. These clones were allowed to grow to reproductive maturity and then harvested. The most significant finding was that ball galled ramets were over twice as likely to be physically isolated from their clone as ungalled ramets (McCrea and Abrahamson, 1985). It comes as no surprise then that we found no significant gallmaker effects on biomass allocation at the clone level in this study or in a field study examining entire clones (Bresticker and Abrahamson, unpublished data). We can conclude that the impacts of the goldenrod ball gallmakers are reduced through localization. However, because the impacts can come early in the development of a genet, ball gallmakers can reduce the number of ramets in the later years of a genet's life and hence can reduce lifetime fitness (McCrea and Abrahamson, 1985).

The detailed studies of the goldenrod ball gall suggest that even though this gallmaker has appreciable impacts at the ramet level, its impacts are negligible in mature clones. Unfortunately, we can not extend these results to other gallmakers. The impact of each species of gallmakers will vary depending upon host clonality, host organs attacked, tissues stimulated, host reactions, gallmaker seasonal cycles, and the degree of mobilization of host resources by the gallmaker. For example, a leaf gallmaker could stimulate an appreciably greater degree of mobilization, since a single leaf may not produce sufficient resources for the gallmaker. The ball gall, as a stem gall, is in an ideal location to simply intercept resources.

We can illustrate this variation in impacts with an example from another stem gallmaker, the tenthredinid *Euura lasiolepis*, which attacks the arroyo willow, *Salix lasiolepis* (Craig et al., in press). Willow tissues, like tissues of many other plants, become less susceptible to galling with aging. However, Craig and his coworkers have shown that heavy sawfly galling stunts or kills growth distal to the gall and stimulates sprouting of previously dormant buds. The resulting young branches keep the clone susceptible to further galling. Craig et al. (in press) have termed this "resource regulation," in that the gallmaker is maintaining or increasing the resources available to its future generations on the same host. Obviously, this sawfly stem gallmaker affects its host in a markedly different manner than the goldenrod ball gallmaker.

There is little question that gallmakers unilaterally adapt to their host, but the question of whether true reciprocal adaptation occurs is still open. The plant defenses that result in the variation observed in host susceptibility to gallmakers (McCrea and Abrahamson, unpublished data), could be the product of "diffuse" coevolution (sensu Futuyma, 1983) rather than true reciprocal coevolution.

If we hope to understand the ecological and evolutionary framework of host plant-gallmaker interactions, we must examine a number of these interactions from the host's perspective. By detailing gallmaker impacts, we will gain important insights into the selection pressures and the resulting evolutionary responses. Gallmaker-plant systems have the potential to yield crucial perspectives on the degree of reciprocal adaptation.

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SIGNIFICANCE OF NUTRITIVE CELLS IN INSECT GALLS

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Abstract.—Nutritive cells are modified, highly nutritious plant cells that line the larval chambers of galls and serve as the insect's sole source of food. The development and characteristics of nutritive cells found in the galls of *Urophora cardui* (L.) on *Cirsium arvense* (L.) Scop., *Hemadas nubilipennis* Ashmead on *Vaccinium angustifolium* Aiton and *Diplolepis polita* (Ashmead) on *Rosa acicularis* Lindl. are discussed.

Insects belonging to the gall-inducing guild have evolved the ability to redirect the growth and differentiation of plant cells near the larval feeding sites into structures which provide shelter and a rich food supply. Galls are specific expressions of the insect's biology and there is a vast literature explaining how insects alter the tissues of their hosts (see Mani, 1965; Maresquell and Meyer, 1965; Rohfritsch and Shorthouse, 1982; Meyer and Maresquell, 1983).

In contrast to most phytophagous insects which move about the outside of their host organs removing large pieces of plant tissues, gall insects are sedentary and feed on modified plant cells that line the interior surface of their larval chambers. These cells, referred to as 'nutritive cells,' are a characteristic feature of most insect galls (Bronner, 1977). Nutritive cells are usually induced from parenchymatous cells near the feeding sites and not only play a key role in larval nutrition, but also are important in gall development and physiology (Rohfritsch, 1971). The purpose of this paper is to describe the characteristics of nutritive cells and to illustrate the variety of ways in which they are derived from plant cells by examining prosoplastic galls induced by *Urophora cardui* (L.) (Diptera, Tephritidae) on *Cirsium arvense* (L.) Scop. (Canada thistle), *Hemadas nubilipennis* Ashmead (Hymenoptera, Pteromalidae) on *Vaccinium angustifolium* Aiton (lowbush blueberry) and *Diplolepis polita* (Ashmead) (Hymenoptera, Cynipidae) on *Rosa acicularis* Lindl. (wild rose).

GALL DEVELOPMENT AND THE CHARACTERISTICS OF NUTRITIVE CELLS

The series of events whereby insects direct the development of prosoplastic galls are broken down into three phases: initiation, growth and maturation (Rohfritsch and Shorthouse, 1982). Initiation is the critical period in gall morphogenesis when the insect usurps the host in controlling development of nearby cells. Plant cells are usually in an appropriate state of plasticity for a short period of time (Rohfritsch, 1980) during which initiation must occur. Thus the insect must synchronize its oviposition and feeding within this period.

Gall insects become enveloped by numerous layers of rapidly dividing and enlarging parenchymatous cells during the gall's growth phase. Cells lining the larval chamber develop into nutritive cells at the beginning of the growth phase while adjoining cells remain parenchymatous and accumulate reserves of starch (Bronner, 1977). Cells near the centre of the growing tissues give rise to vascular tissues which join those of the host organ. The maturation phase is marked by a cessation of gall growth; however, differentiation of gall tissues continues. A layer of lignified cells called the hard or sclerenchyma layer appears beyond the starchy reserve layer (Fourcroy and Braun, 1967). Enlarged cortical parenchyma cells beyond the hard layer contain large vacuoles and are thought to act as water storage (Maresquelle and Meyer, 1965). Most larval feeding occurs during the gall's maturation phase.

Nutritive cells in the galls of most insects are characterized by dense cytoplasm, fragmented vacuoles, enlarged nuclei and nucleoli and abundant organelles including ribosomes, plastids and mitochondria. They also contain high concentrations of sugars, proteins and RNA (Bronner, 1977). Cells lining the larval chamber are usually without starch. However, the adjoining parenchymatous cells contain starch in increasing amounts towards the gall periphery. There also is a lipid gradient but it runs opposite to the starch gradient (Bronner, 1977). Thus gall insects, via their nutritive cells, exert a mobilizing effect on their hosts bringing about a relocation of nutrients and in doing so ensure a continuous supply of high quality food. Nutritive cells also play a critical role in the harmonious development of galls and retain their characteristics only if the larvae continue to feed. Death of the larvae due to parasitism, for example, results in a rapid loss of cellular characteristics and further events in gall morphogenesis cease (Rohfritsch, 1971).

Some authors refer to all tissues found between the larval chamber and the lignified sheath as nutritive tissue since all cells in this region are destined to develop the features of those lining the larval chambers. Bronner (1977) divided the nutritive tissue into two parts, the inner part referred to as 'typical nutritive tissue' and the outer part as 'storage nutritive tissue.' In the present paper, only the cytoplasmically dense cells lining the larval chamber are considered nutritive cells. Cells between the nutritive layer and the lignified sheath are considered gall parenchyma.

GALL OF *UROPHORA CARDUI* ON *CIRSIIUM ARVENSE*

Figs. 1-2, 7-9

Urophora cardui has been extensively studied as a result of its importation from Europe into Canada for biocontrol of Canada thistle (Peschken and Harris, 1975; Lalonde and Shorthouse, 1984). The mature gall is spherical to oblong (Fig. 1) and is induced from stem tissues. It is multi-chambered with each larva in its own chamber (Fig. 2). Structurally the gall is unique since it has two types of nutritive cells referred to as primary and secondary nutritive cells (Lalonde and Shorthouse, 1984).

Eggs are laid in the vegetative shoots and when the second instar larvae hatch, they tunnel into the stems to a region where differentiation of vascular tissue is beginning. Tunnelling produces a wound reaction filling the tunnels with callus thus sealing the larvae within plant tissues. Initiation of the gall begins when pith



Figs. 1-6. 1, Mature gall of *Urophora cardui* on the main stem of Canada thistle ($\times 1.5$). 2, Dissection of mature gall of *U. cardui* with fully grown larvae ($\times 6$). 3, Mature gall of *Hemadas nubilipennis* on adventitious shoot of lowbush blueberry ($\times 2$). 4, Dissection of mature gall of *H. nubilipennis* ($\times 4$). 5, Cluster of mature galls of *Diplolepis polita* on the leaflets of wild rose (natural size). 6, Dissection of mature gall of *D. polita* ($\times 8$).

and procambial tissues near the larvae begin to proliferate producing gall parenchyma around the larval chambers. As the gall enters the growth phase, gall parenchyma divides rapidly surrounding the larvae with thick masses of cells. Primary nutritive cells are differentiated from gall parenchyma along the base of larval chambers early in the growth phase (Fig. 7). They appear in irregular patches from 2 to 10 cells thick with each cell exhibiting the characteristic dense cytoplasm and enlarged nucleus.

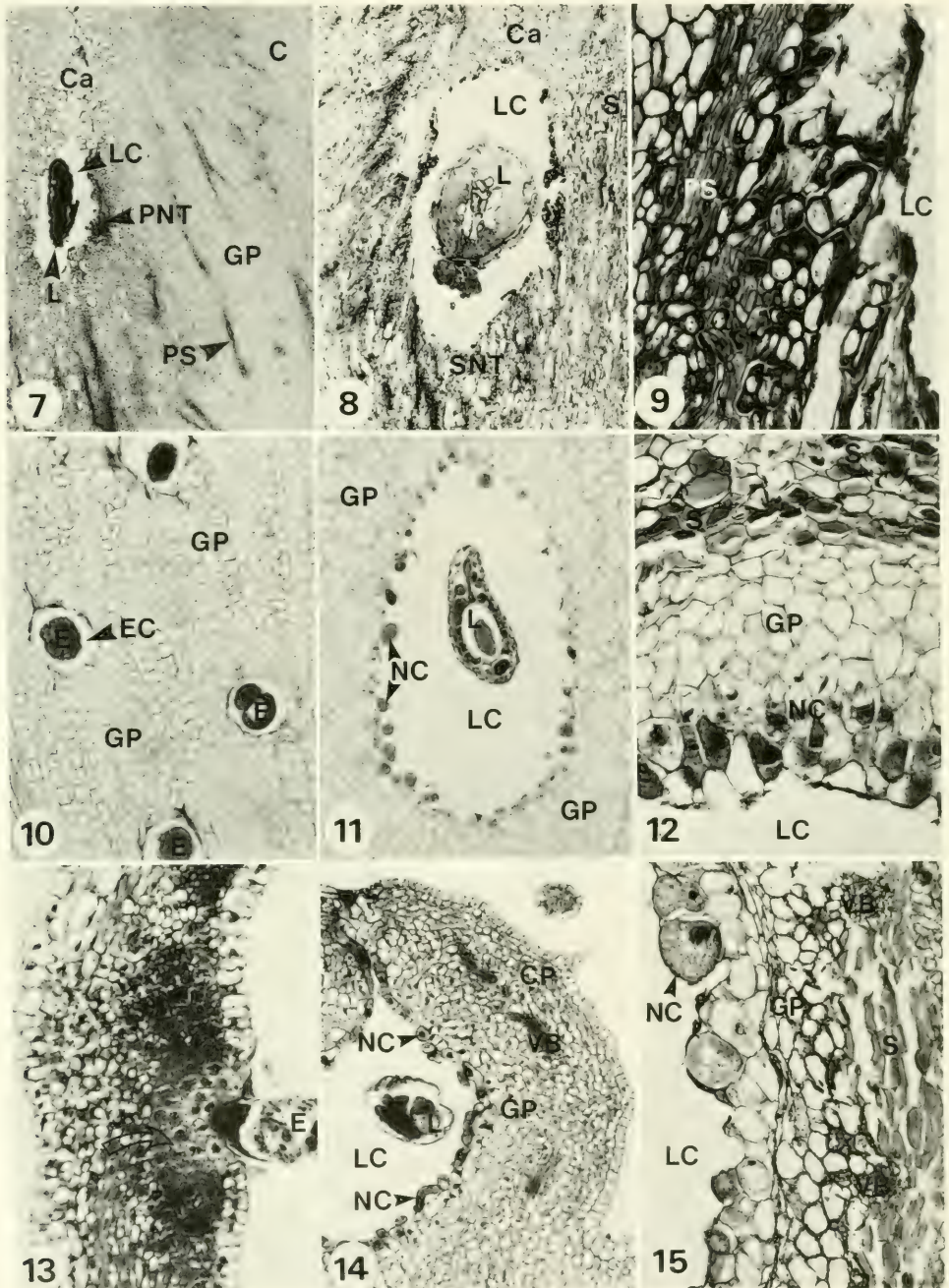
The gall grows rapidly during the growth phase then abruptly slows at the beginning of the maturation phase (Lalonde and Shorthouse, 1985). The sluggish larvae remain in the second instar throughout the growth phase and grow slowly. Once sufficient gall parenchyma has accumulated by the end of the growth phase, the larvae induce the formation of secondary nutritive cells and begin feeding vigorously. The larvae moult to the third instar once secondary nutritive tissue appears. Secondary nutritive cells first appear near procambial strands when primary nutritive cells are still present. However, soon after the onset of gall maturation, all primary nutritive cells are consumed and the larvae are surrounded by secondary nutritive cells (Fig. 8) except for the callus plug at the apex which is to serve as the adult's escape route.

Secondary nutritive cells appear by additive divisions of procambial cells which act as initials. Each derivative cell enlarges tangentially so a gradient of increasing cell size appears away from the procambial initials to the larval chamber (Fig. 9). Secondary nutritive cells have a large central vacuole and an elongate shape; they are rich in protein and lipid-like globules (Lalonde and Shorthouse, 1984). All gall parenchyma beyond the secondary nutritive tissue lignifies. All secondary nutritive cells are consumed by the end of the maturation phase leaving the larval chambers lined with lignified cells (Fig. 2). It appears that the primary nutritive cells are regulatory centres for gall growth and development, whereas the secondary nutritive cells serve to transfer nutrients to the larvae (Lalonde and Shorthouse, 1985). Second instar larvae are essentially non-feeders responsible for directing plant biomass around themselves, whereas the third instar is responsible for food consumption and growth.

GALL OF *HEMADAS NUBILIPENNIS* ON *VACCINIUM ANGUSTIFOLIUM*
Figs. 3–4, 10–12

Hemadas nubilipennis Ashmead is the only nearctic member of the family Pteromalidae with the ability to induce galls. Its galls are induced on lowbush blueberry, a deciduous perennial native to northeastern North America. Mature galls are reniform or globular and usually are found at the tips of adventitious shoots (Fig. 3) which arise from buds on rhizomes. Mature galls are multichambered with chambers arranged in rows (Fig. 4); only one larva is found in each chamber.

The life cycle of *H. nubilipennis* has been described by West (1983). Females oviposit into undifferentiated tips of adventitious shoots while the shoots are still within the leaf litter (Shorthouse et al., 1986). Eggs are deposited in vertical rows at the end of oviposition channels and are placed such that they transect the procambial strand distal to the point of entry. Gall initiation occurs before the eggs hatch. The egg stage lasts for approximately 14 days, but during this period tissues surrounding the egg chambers undergo rapid cell divisions. The female



Figs. 7-15. Sections of galls of *Urophora cardui* (7-9), *Hemadas nubilipennis* (10-12) and *Diplolepis polita* (13-15). See Lalonde and Shorthouse (1984) for techniques used in sectioning and staining. 7, Longitudinal section of *U. cardui* gall in early part of growth phase ($\times 25$). 8, Longitudinal section of *U. cardui* gall in mid-maturation phase ($\times 23$). 9, Longitudinal section of maturing secondary nutritive cells lining larval chamber of *U. cardui* gall ($\times 160$). 10, Longitudinal section of adventitious shoot inhabited by eggs of *H. nubilipennis* 10 days after oviposition ($\times 90$). 11, Cross section of *H. nubilipennis* gall in early growth phase ($\times 90$). 12, Cross section of *H. nubilipennis* gall in maturation phase showing

also stabs the shoot apex after oviposition and growth of the shoot stops. Shorthouse et al. (1986) suggested that larvae and gall tissues become physiological sinks with all nutrients normally destined for shoot growth are instead going to the gall.

Cells surrounding the eggs begin to divide within 48 hours of oviposition becoming the gall parenchyma and, after 10 days, thick layers of uniform, compact gall parenchyma surround each egg (Fig. 10). Cells closest to the eggs are arranged in a radial pattern about the egg chambers (Fig. 10). Freshly hatched larvae begin feeding on gall parenchyma and within 5 days small clumps of nutritive cells are induced along the inside surface of the chambers. Hatching of the eggs approximates the end of the initiation period. Gall parenchyma continues to proliferate and enlarge the gall during the growth phase, which lasts from 60 to 70 days. Nutritive cells, all of which are derived from gall parenchyma, continue to arise and by day 20 form a discontinuous layer around the chamber surface (Fig. 11). The layer is continuous after 40 days. Procambial strands found throughout the gall parenchyma during the growth phase form horizontal anastomoses with the unaffected portion of the vascular cylinder. By the end of the growth phase the nutritive layer is up to 7 cells thick and as the gall enters the maturation phase a sheath of sclerenchyma cells appears lying contiguous to the vascular tissue. The larvae feed most actively during the maturation phase and the zone of parenchyma becomes much reduced (Fig. 12). All nutritive and gall parenchyma are consumed by the end of the maturation phase and the larval chambers become encapsulated by the hard sclerenchyma sheath. Only a thin layer of sclerenchyma separates the larval chambers (Fig. 4) as the mature gall becomes woody and ready for winter.

GALL OF *DIPLOLEPIS POLITA* ON *ROSA ACICULARIS*

Figs. 5–6, 13–15

Diplolepis polita is one of the most widely distributed of the approximately 28 species of nearctic *Diplolepis*. It has been found across central Canada from British Columbia to Quebec and north to central Yukon and Alaska. Mature galls are spherical and spinulose (Fig. 5) and are found in clusters on the adaxial surface of the leaflets of *Rosa acicularis*. Only one larva is found per gall (Fig. 6). The life cycle and ecology of *D. polita* and other inhabitants of the gall have been described elsewhere (Shorthouse, 1973, 1980).

Eggs of *D. polita* are laid individually in the early spring on leaflets still folded within leaf buds. Only a few epidermal cells are damaged by oviposition along with a small cluster of cells beneath the egg which begin to lyse. Cells next to the lytic zone become highly stimulated within 48 h developing enlarged and fragmented vacuoles. These cells begin to proliferate giving rise to a small pad of tissues (Fig. 13) and as they expand around the lytic tissues they form a slight

←

thick layers of nutritive cells lining a larval chamber ($\times 150$). 13, Section of egg of *D. polita* and host leaflet 48 hours after oviposition. Note pad of stimulated cells (arrow) beneath the egg ($\times 400$). 14, Cross section of *D. polita* gall in growth phase ($\times 115$). 15, Cross section of *D. polita* gall in maturation phase ($\times 120$). C, cortex; Ca, callus; CP, cortical parenchyma; E, egg; EC, egg chamber; GP, gall parenchyma; L, larva; LC, larval chamber; NC, nutritive cell; PNT, primary nutritive tissue; PS, procambial strands; S, sclerenchyma; SNT, secondary nutritive tissue; VB, vascular bundles.

cavity beneath the egg. The egg hatches within 5 days of oviposition and the larva moves into the cavity.

The initiation phase ends as the larva begins to feed. The larva is surrounded by plant tissues within 8 days of oviposition and soon after cells lining the larval chamber develop into nutritive cells (Fig. 14). A new cambial zone forms within the gall tissues midway between the larval chamber and gall exterior and from these cells gall parenchyma proliferates towards the larval chamber and cortical parenchyma towards the exterior. Gall parenchyma near the larval chamber develops into nutritive tissue, whereas the cortical parenchyma accumulates starch granules. Vascular tissues appear within the cortical tissue (Fig. 14) early in the growth phase and connect with vascular bundles of the host organ. The growth phase lasts for about 20 days.

The maturation phase begins when a layer of cells near the vascular bundles, midway between the larval chamber and gall exterior, begin to lignify. The cortical cells lose their starch granules, but the gall parenchyma continues to give rise to nutritive cells. As the sheath of sclerenchyma cells develops, the gall becomes a series of concentric layers (Fig. 15). Nutritive cells of the maturing gall are the largest cells of the gall (Fig. 15) and have the typically dense cytoplasm and enlarged nuclei. Later in the maturation phase, gall parenchyma inside the sclerenchyma sheath develops into nutritive tissue faster than it can proliferate and thus decreases in thickness. The larva consumes all nutritive cells and gall parenchyma late in the maturation phase, which is about 45 days after oviposition, and the larval chamber becomes lined with the sclerenchyma sheath.

DISCUSSION

The three galls described in this paper are useful models for examining the complex relationships between gall insects and their host plants. They also illustrate how gall ontogeny varies between various groups of gall inducers. Emphasizing the nutritive cells also draws attention to the unique feeding habits of gall insects. No other group of phytophagous insects is able to remain in one feeding site on a host organ and stimulate the plant into supplying it with a steady stream of highly nutritious substances. Nutritive cells are the sole source of food for gall insects and they act as physiological sinks drawing nutrients to the surface of the larval chambers from regions of the plant some distance away. They also influence the composition of nutrients passing through the gall to the larvae.

There are hundreds of insect-induced galls whose structures and the feeding habits of insects within remain unstudied. Perhaps when we determine how more of these systems develop and function, gall studies will make a significant contribution to our understanding of the organic relationships between plant and animal cells.

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GALLS IN HARSH ENVIRONMENTS

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Abstract. — Responses of various gallforming species to environmental stresses are evaluated on three scales of variation: geographical, within habitat, and within plant. Along elevational gradients, species diversity and densities decline at higher elevations. Within habitats, gall densities are lower on water stressed plants, in most cases. Within plant variation in branch age and vigor also elicits strong gallformer responses, although responses to this factor are more variable between species. Elevational gradients, local plant quality and within plant quality, considered collectively, are good predictors of how gall systems will be organized.

A variety of environmental stresses or harsh conditions operate on different scales to organize biological communities in nature. This paper considers three such scales of variation and their effects on gallforming herbivores: 1, elevational gradients, which give rise to heat and cold stresses at opposite ends of the gradient and may encompass hundreds of kilometers of host plant range in scale; 2, within habitat or locally stressful conditions, such as plant water stress and nutrient stress, which involve smaller populations of plants; and 3, within plant quality, where aging of individual branches modifies their value as resources, involving dynamics of individual plants. These three scales of stresses can affect the survivorship and fitness of herbivores directly, and also indirectly, by changing the quality of the resource—the host plant, with which the herbivore interacts in an intimate fashion.

There are several important reasons for understanding gallformer responses to these scales of variation: first, to see if gallformers exhibit a common response to environmental stresses. This would determine whether gallforming, as a form of herbivory, has a really unique and readily understood ecology, or if gallformers are as variable in their responses to environmental qualities as are other types of herbivores. One could reasonably predict common responses by gallformers across taxonomic lines because they all share several fundamental biological features, perhaps the most important being their dependence on vigorously growing, meristematic plant tissue to initiate gall development and ensure survival of their progeny.

These results may also be of more general value: By understanding how a species or group of species responds to variable conditions occurring biogeographically, within habitats and within plants, one could predict a great deal about how a biological community or portions of it will be organized at any point in space.

To address this I interviewed researchers working on a variety of gallforming

Table 1. Biogeographical patterns in gallforming herbivores.

Author, Plant	No. Gall Species	Elev. Range Con- sidered	Species Response	Numerical Response
1. Sacchi,* <i>Salix</i> sp.	4	1690–2460 meters (M)	1 sp. drops out at 2460 M	no change
2. Hawkins et al. (1986), <i>Atriplex</i> spp.	8	low desert to 1690 M	3 spp. drop out in Mohave	many rare
3. Hartman (1985), <i>Tetradymia</i> sp.	>1	1122 to 1268 M	?	most rare
4. Fernandes,* many species	13	308 to 3877 M	only 1 spp. above 2770 M	?
5. Fay,* <i>Picea</i> sp.	1	2460 to 3570 M	—	rare above 3077 M
6. Waring,* <i>Larrea</i> sp.	11	277 to 1138 M	7 species drop out above 923 M	most rare

* = unpublished data.

systems to determine how the herbivore(s) of interest respond to environmental stresses.

RESULTS AND DISCUSSION

Species diversity in the four multispecies gall systems considered declined as species dropped out with increasing elevation (Table 1) (no information on species responses was available from Hartman (1985), #3, and Fay, #5, is studying only one species). The result of this pattern is that community diversity will be lower at higher elevations.

Gallformer abundance, another component of community makeup, is also highly correlated with elevational change. In 4 of 5 systems for which density information was available, densities declined with increasing elevation (Table 1).

These results indicate that elevation, with the climatic features which accompany it, is a good predictor and determinant of species diversity and density in gallforming systems. Ultimately, two features of elevation may be operating to cause these patterns: gallforming may be especially adaptive at drier, lower elevations, where herbivores are exposed to strongly dessicating conditions, and nonadaptive at higher elevations due to prohibitively cold temperatures and reduced productivity in plants.

Decreasing species diversity at higher elevations and latitudes within the *Asphondylia* (Diptera: Cecidomyiidae) guilds on both *Atriplex* spp. and *Larrea tridentata* (DC.). Coville suggests that this pattern, when observed in gall studies where more than one host plant species is involved, is not merely a response to a decrease in host plant species across these gradients. The influence of climatic change on the radiation of these gallforming species deserves further consideration.

Within habitats, variability in plant water stress strongly affects gallformer distributional patterns (Table 2). In 4 of these 6 gallformer systems, fewer gallformers colonized water stressed plants, indicating that well watered, vigorously growing plants are preferred resources. In one case (Table 2, #1), survivorship was greater on well watered plants, indicating that well watered plants are also better resources for some gallformers.

Table 2. Gallformer responses to plant quality.

Author, Plant	Gallformer	Response to Stress		Nature of Response
		Water	Nutri.	
1. Price and Clancy (1986), <i>Salix</i> sp.	<i>Euura lasiolepis</i> Smith	—	—	reduced #'s and survivorship
2. Fay,* <i>Picea</i> sp.	<i>Adelges cooleyi</i> Parry	—	?	reduced #'s
3. Abrahamson,** <i>Solidago</i> sp.	<i>Eurosta solidaginis</i> (Fitch)	—	—	?
4. Hawkins et al., (1986) <i>Atriplex</i> spp.	<i>Asphondylia</i> spp.	—	?	reduced #'s
5. Waring,* <i>Larrea</i> sp.	<i>Asphondylia</i> spp.	+	?	increased #'s
6. Clancy,* <i>Salix</i> sp.	<i>Pontania pacifica</i> Marlatt	+	—	improved survivorship

* = unpublished data.

** = personal observation.

This pattern is not surprising because well watered plants grow more vigorously than do stressed plants, which may explain why they are better resources for many gallformers. The preference for water stressed plants in 2 cases (Table 2, #5 and 6) is enigmatic in light of this.

All gallformer species responded strongly to the condition of water stress in plants, regardless of the nature of the response itself. The number of species of *Asphondylia* was greater on stressed creosote bushes (Waring, unpublished data), so species diversity as well as densities are affected by plant water stress. The *Asphondylia* species colonizing *Atriplex* responded differently to water stressed plants by colonizing them less than well watered plants. Such a discrepancy within a gallforming genus suggests that the species of host plant involved is also an important determinant of herbivore response (Table 2). Likewise, within the willow system, the 2 colonizing sawflies (Table 2, #1 and 6) responded differently to water conditions within the same plant species (*Salix lasiolepis* Benth), with *Euura lasiolepis* Smith (Hymenoptera: Tenthredinidae) colonizing stems on well watered plants and *Pontania pacifica* Marlatt (Hymenoptera: Tenthredinidae) colonizing leaves on water stressed plants. Both species survived more frequently on their respective plant types (Table 2). Clearly, the relationships of these herbivores and host plants are complicated, but the responses to plant water conditions are strong enough that an understanding of existing water conditions enables one to predict densities, species diversity and levels of survivorship in many gallforming systems within habitats.

A wide taxonomic range of gallformers responded strongly but variably to changes in within plant quality. In 4 of 6 cases gallformers were more abundant, and in one case, had increased survivorship on younger, vigorously growing branches (Table 3). In contrast, 2 other systems responded negatively to increased vigor with lower densities and survivorship (Table 3). In the *Asphondylia* guild on creosote bush, fewer species as well as individuals occurred on vigorously growing branches (Waring, unpublished data). So diversity and densities of gallformers vary considerably within plants due to this quality alone. In all systems,

Table 3. Gallformer responses to within-plant quality.

Author, Plant	Gallformer	Prefers Vigorous Growth	Response
1. Thoeny,* <i>Robinia</i> sp.	<i>Ecdytolopha insiticihana</i> Zeller	yes	increased #'s
2. Washburn and Cornell (1981), <i>Quercus</i> sp.	<i>Xanthoteras politum</i> (Bassett)	yes	increased #'s
3. Craig et al., (1986), <i>Salix</i> sp.	<i>Euura lasiolepis</i>	yes	increased #'s and survival
4. Frankie and Morgan (1984), <i>Quercus</i> sp.	<i>Disholcaspis cinerosa</i> Bassett	yes	increased #'s
5. Kearsely,* <i>Populus</i> sp.	<i>Pemphigus betae</i> Doane	no	decreased #'s and survival
6. Waring,* <i>Larrea</i> sp.	<i>Asphondylia</i> spp.	no	decreased #'s

* = unpublished data.

individual branches within plants increase or decrease in their susceptibility to galling as they age, with the direction of the response dependent on the system.

These galls became scarce at the upper ends of elevational gradients and locally on water stressed host plants, in most cases. All species responded strongly to within-plant changes, although the direction of the response varied. More studies must be undertaken to verify these patterns. In general, gallformers responded negatively to environmental and biotic stresses.

Elevational, within-habitat and within-plant stresses are straightforward and fundamental factors and are useful in understanding the dynamics of gall systems. In the case of *Asphondylia* spp. on creosote bush, for instance, the densities and numbers of these species will be greatest at lower elevations, on water stressed plants and in the older, less vigorous portions of plant canopies. Although these three levels or scales may operate differently, they will have the same effects on populations, such that more stress equals more galls and species. Consideration of each level adds more resolution to an understanding of how biological communities or portions of them will be organized.

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THE TRANSITION FROM FUNGUS-FEEDING TO PLANT-FEEDING IN CECIDOMYIIDAE (DIPTERA)

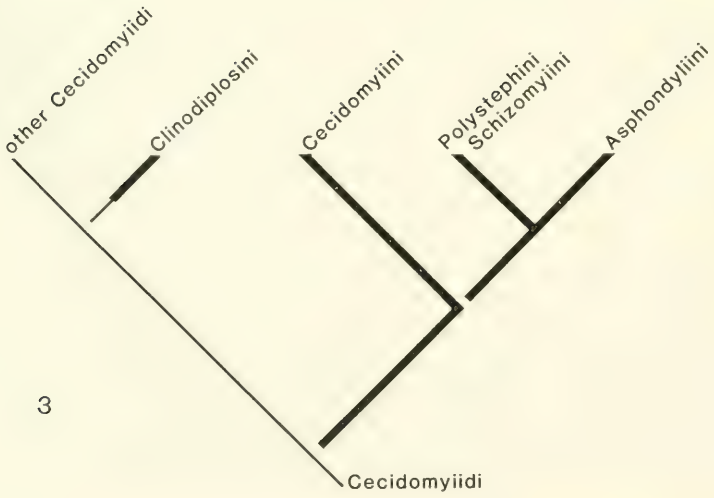
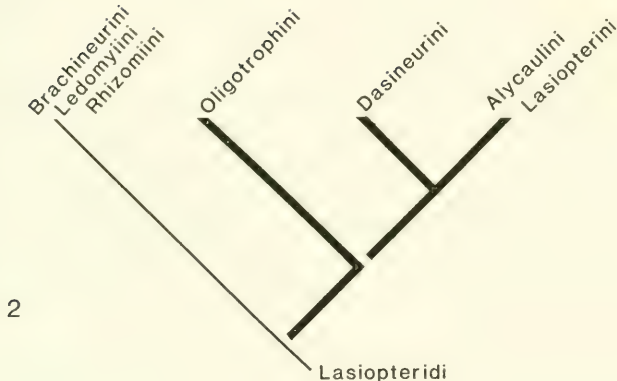
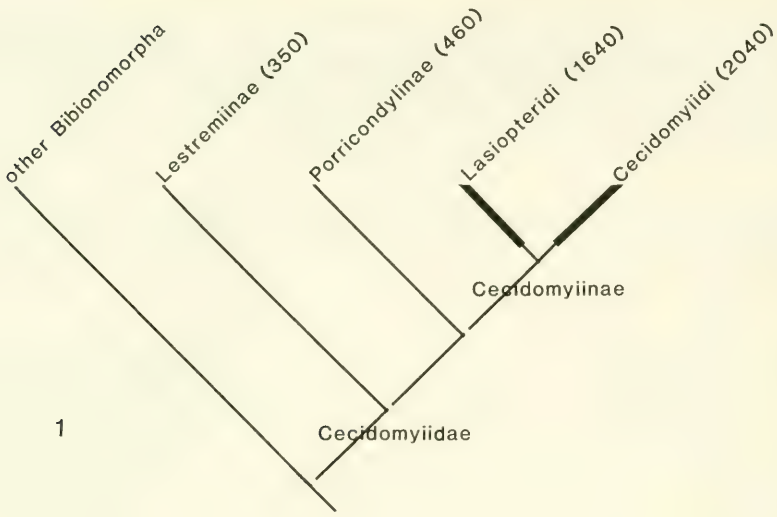
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Abstract.—A speculative inquiry is made into the change in Cecidomyiidae from the ancestral fungus-feeding habit to the plant-feeding habit. Plant-feeding in these insects has apparently evolved separately at least three times. The greatest change necessary in switching to plant-feeding was in the salivary secretions, which cause the plant to react by producing food and gall tissue. Anatomical modifications needed for sucking plant juices and digging into soil were already present in fungus-feeding cecidomyiids and preadapted them for plant-feeding.

Enough is known about Cecidomyiidae to sketch a broad evolutionary outline of its groups and their relationships (Fig. 1). Primitive cecidomyiids are fungus-feeders and evolved from fungus-feeding land midges. Plant-feeding is a relatively recent habit in Cecidomyiidae and has probably developed separately in the family at least three times (Figs. 2-3). Where that habit developed, there followed a great increase in the number of species, presumably because of the host-specificity that follows the synchronization of the biology of most gall midges with their individual hosts.

Cecidomyiid larvae are legless, more or less cylindrical, and taper anteriorly to the tiny head, which is much reduced in size compared to that of other Nematocera. Ancestral fungus-feeding Cecidomyiidae developed unique adaptations that preadapted their larvae for plant-feeding. Most of these modifications affected the feeding apparatus of the larvae. The structure of the larval head has been studied in detail by Solinas (1968, 1971). Larvae feed by appressing the cone-shaped head to the food source, exerting the mandibles that pierce and hold fast or scrape the substrate, and immediately discharging salivary secretions. The muscles of the head capsule dilate the esophagus and the predigested fluids are ingested. The salivary glands of all cecidomyiid larvae are large relative to their body size (Mamaev, 1975). Ancestral cecidomyiids also evolved a prothoracic dermal structure called the spatula that appears on the last larval instar, sometimes also the penultimate instar. This organ serves to take over the function of digging from the reduced head. In some plant-feeding gall midges the spatula is used for cutting through woody tissue; in others it is lost. Changes in the feeding apparatus of more advanced, plant-feeding cecidomyiids are relatively minor and differ in detail only. As examples, mandibles become modified for various specific uses (Solinas, 1971), intestines become simplified in plant-feeders (Mamaev, 1975), and spatulae are used for purposes besides digging and are often lost.



Not only must larval salivary secretions of plant-feeding gall midges be specific to stimulate plant growth, but adults must synchronize their emergence, mating, and egg laying with development of suitable tissues by the host plants. Gall midge larvae do not bore into plant tissue. Usually, the female lays eggs on or among plant surfaces, and the larva, upon hatching, crawls to a suitable site, which always involves meristematic tissue, settles, and begins feeding. Spence (1969) and Rohfritsch (1980) have shown that once a larva settles, the body form changes so that the larva can no longer crawl. The plant then grows quickly around the larva, forming a gall.

Two supertribes contain plant-feeding gall midges (Fig. 1). In the Lasiopteridi (Fig. 2) the most primitive tribes are fungus-feeding and species poor. Plant-feeding probably developed once in this supertribe. All four of the plant-feeding tribes occur on a great variety of plants. Many Oligotrophini produce structurally complex galls, although some species produce simple leaf or bud galls. Some Dasineurini live freely in flower heads but most form simple galls: rolled or swollen leaves, swollen buds, and stems. The Alycaulini and Lasiopterini, chiefly stem gallmakers, have regained a relationship with fungi. Their fungal associates begin growth as a white mycelial mass that ultimately surrounds the larval nidus with a black excrescence which, at about the time the gall midge larvae are full grown, forms a cast around the larvae or their tunnels. In some cases the fungus covers a much more extensive area than that occupied by the larva. For example, the larva of *Asteromyia carbonifera* (Osten Sacken) in a leaf blister gall is stationary and the area immediately surrounding its head remains green until the larva is full grown. Many of these Lasiopterini do not appear to feed on the fungus. In fact, some species, e.g. *Asteromyia modesta* Felt, live in leaf blister galls without a fungal associate (Gagné, 1968).

Primitive members of the supertribe Cecidomyiidi, in the branch labeled "other Cecidomyiidi" in Fig. 3, comprise many kinds of general and specific fungus-feeders, as well as species that are predatory on insects and mites, a habit that evolved at least three times in this supertribe. Most Clinodiplosini in the Holarctic Region are polyphagous fungus-feeders, but some appear to be monophagous fungus-feeders and a few feed in and kill plant buds. In the Neotropical Region, however, many species form complex galls and are host specific.

The other plant-feeding Cecidomyiidi are extremely diverse and rich in species and occur on most groups of gymnosperms and angiosperms. Some live freely in flower heads but most form simple and complex galls. One tribe, the Asphondyliini, which occurs throughout the world on certain groups of angiosperms, has regained a relationship with fungi. Unlike most other cecidomyiids, these gall midges insert their eggs directly into the plant by means of a long needle-shaped ovipositor. It is possible that ovipositional fluid from the female initiates gall formation. The larvae move inside their individual cells and evidently feed on the fungus that grows evenly about the interior surface. Plants affected by As-

←

Figs. 1–3. Simplified phylogenetic trees of Cecidomyiidae. Thickened lines indicate plant-feeding groups. Breaks in lines indicate that the basal line is paraphyletic to what follows. 1, Subfamilies and supertribes with number of valid species presently known. 2, Tribes of Lasiopteridi. 3, Tribes of Cecidomyiidi.

phondyliini produce galls that are unique among all other cecidomyiid galls in that they have no nutritive cell layer (Ross, 1932).

In summary, the transition from fungus-feeding to plant-feeding required many modifications to adapt gall midge biology to that of plant phenology and physiology, but the basic adaptations, sucking mouthparts, extraintestinal digestion, and spatula, needed to begin the process were already in place. The most important subsequent changes had to occur in the salivary secretions to make the host plant tissue react to feed the larva. Since plant-feeding mechanisms evolved independently several times, one can suppose that the requisite genetic changes were relatively few. The feeding apparatus of gall midges is a development analogous to that of the cephalopharyngeal skeleton of higher Diptera. In both groups those developments were the precursors of explosive evolution.

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THE FOSSIL GALL RECORD: A BRIEF SUMMARY

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Abstract.—The current status of the fossil gall record is discussed. Significant specimens are highlighted. Despite limitations of the record, available specimens indicate that the gall-forming habit in insects developed to richness in the Tertiary with several relationships stable since the Pliocene (13 mya). Apparent lacunae in the record are discussed.

The history of galls and gall formers has been studied using at least two approaches. The first is to consider the present day distribution of gall-forming insects in light of what is known about land mass distribution and movement. This paleobiogeographic method may provide information needed to reconstruct events without reliance on the admittedly spotty fossil record. For example, the most thorough paleobiogeographic examination of an extant gall-forming taxon suggests a constancy in morphology and habit since the Eocene (50 million years ago) in a species of seed and bract galling cecidomyiid (*Semudobia skuhravae* Roskam) (Roskam, 1979; Gagné, 1984). Once evidence from both biogeography and fossils is brought to bear on the *same* examples, we can expect more complete reconstructions than are presently possible using either tool alone.

As indicated, the second approach to studying gall history is to examine the fossil record. Although several (25 total) accounts of fossil galls have been published, no examination of the assembled record has been made. The purpose of this and another paper (Larew, (a) in press) is to provide a brief summary using paleobotanical evidence of the fossil gall record's status and implications. The fossil record may provide minimum ages of gall-forming associations. Ideally, it may also indicate whether the composition and richness of gall-forming taxa have changed over time.

We are undoubtedly biased in our search for and study of fossil galls. We may for example assume that galls of the past looked like those of today, and pass over or be unable to interpret abnormal structures from plant fossils that were in fact galls. Thus our interpretation of the record may be skewed to infer stability of relationships. There are weaknesses in the fossil gall record itself. For example, almost all known fossil galls are two dimensional impressions in which neither the gall-former nor detailed gall structure is preserved. The identity of the preserved host plant or the age of the specimen may be unclear. Descriptions of the specimens or the specimens themselves are often not of the detail or clarity to distinguish a gall from an artifact of preservation. Lastly there is a scarcity of described specimens.

Despite these limitations fossil galls that have been described provide a skeletal history of gall formation. What follows is a brief review of the highlights of the fossil record. For a more complete description, see Larew ((a), in press).

The oldest known gall was described by Weiss (1904) from tissue sections of *Stigmaria*, which is the root of extinct club moss trees such as *Lepidodendron*. The specimen is from England and is of early Carboniferous age (315 million years ago). Based on the anatomy of root tissue swelling and on the hypertrophied spore-bearing cell in the swelling, Weiss named the gall-former *Urophlyctites stigmariae*, which indicates the similarity in damage seen in the specimen to that caused by the extant chytrid fungus, *Urophlyctis*. Apparently a *Urophlyctis*-like fungus survived the extinction of *Stigmaria/Lepidodendron* and occurs today on the roots of swamp plants and on plants that are periodically flooded such as *Medicago* (Alexopoulos, 1962).

The oldest suspected insect-caused galls are approximately 115 million years old from the upper Cretaceous of Maryland, USA, and were described by Hickey and Doyle (1977) as impressions of leaves of "Sassafras" (there is uncertainty about the host plant's identity although it may be allied with the Platanales). I have found a total of 49 of these galls on leaves collected by Hickey and Doyle. In size, suggested structure and pattern of incidence on the leaves these circular impressions resemble modern day oak leaf spangle galls that are caused by cynipid wasps. The fact that the identity of the fossil host plant is unclear and that oaks are not known from the upper Cretaceous precludes statements about the longevity of this particular relationship. The specimens, however, are significant in their suggestion that structurally sophisticated insect-caused galls were present at a relatively early date.

The most valuable fossil galls are those that were found in the "Miocene (?) (25 million years ago) lignites of the Duren mines in West Germany (Möhn, 1960). They are noteworthy because larval and pupal cecidomyiids were found in the gall; the larvae lived in, fed on and presumably galled the seeds within the cones of *Sequoia langsdorffii*. Extant *Sequoia* do not host seed-feeding or galling cecidomyiids. The closely related genus *Taxodium* does (Gagné, 1968). Thus the fossil midge species did not survive the reduction in *Sequoia*'s range, but a closely related midge species survives on a related host plant (Gagné, 1968).

The largest collection of fossil galls (Straus, 1977) includes 34 types of leaf gall impressions from the Pliocene (13 million years ago) of West Germany. Included are 2 fungal, 12 eriophyoid, 1 eriosomatid, 1 aphid, 1 adelgid, 6 cecidomyiid, and 3 cynipid galls and 8 of unknown origins. In 13 cases Straus assigns the fossil gall former to extant genera or species. If he is correct in his identifications then it can be concluded that there was a rich and recognizable gall-forming fauna in the Pliocene on several of the plants that are attacked today.

Recently preserved galls, i.e. those preserved in the last 2 million years, include 2 cynipid-caused acorn galls preserved approximately 15,000 years ago in the La Brea tar pits, Los Angeles, California, USA (Larew (a), in press), and are the only known fossil galls of angiosperm seeds. Even more recently preserved were the cynipid-caused oak leaf galls carbonized and thus preserved at Herculaneum, an Italian city destroyed by the eruption of Mount Vesuvius in A.D. 79. Although these last galls are only about 1900 years old, they are nonetheless significant in that they provide the first tangible clues to the importance of galls in early human

Table 1. Geologic time table with the numbers of galls per period or epoch shown, and gall events given in relation to paleobotanical and paleoentomological events.

Period/Epoch	Beginning of Interval (Millions of Years Ago)	Event	Galls	Gall Event
Holocene	0.01		13	All <i>Quercus</i> /cynipid
Pleistocene	1.5–2		3	
Pliocene	5–13		28	Many recognizable galls
Miocene	22–23		7	
Oligocene	37–38		6	
Eocene	53–54	Modern angiosperms	4	
Paleocene	65			
Cretaceous	136	First angiosperms	6	First insect gall
Jurassic	195		1	
Triassic	225	Abundant cycads and conifers		
Permian	280			
Carboniferous	345	Abundant insects and coal forest	1	First gall (fungal)
Devonian	395	First insects		
Silurian	435	First land plants		
Ordovician	500			
Cambrian	570			
Total			69	

culture. Collection data suggest that the galls were being offered for sale in a shop probably as a source of tannins for medicines or dyes, at the time of the eruption (Larew (b), in press).

A summary of major paleobiological events is shown in Table 1. The number of fossil gall specimens in each period or epoch is provided as are comments about particular specimens. In general the record suggests that as early as the late Paleozoic (Carboniferous), cecidogenetic relationships existed that resemble those that occur today. The gall-forming habit in insects, although seen probably as early as the Cretaceous developed to richness in the Tertiary (the Pliocene, especially) when modern day angiosperms became abundant. From the Pliocene, indications are that many relationships have been stable. According to Opler (1973) fossil evidence of lepidopterous leafminers on oaks demonstrate a similar constancy from the middle Miocene.

There are noticeable lacunae in the fossil gall record. For example, there are no known fossil galls from regions other than western Europe and the United States. This deficiency may in part explain why there are no fossil galls that have been ascribed to thrips or scales; galls caused by these insects are most common today in Asia and Australia. Neither are there reports of fossil galls caused by beetles or moths, despite the suggestion that structurally these are some of the simpler and presumably more primitive insect galls today (Mani, 1964). No fossil flowers or stem galls have been described.

Lastly, although the first land plants are known from the Silurian, the first gall (*Urophlyctites*) does not occur until the Carboniferous, approximately 150 million years later. Was there a time lag of many millions of years between the devel-

opment of a terrestrial flora and the first occurrence of galls? Or is the fossil gall record incomplete? The last seems more likely. Just as curious is the complete lack of gall specimens from aquatic plants *before* the Silurian. Algae, bacteria, fungi, nematodes, rotifers and copepods form galls on marine and fresh water algae today (Mani, 1964). Although insects presumably arose in the Devonian, insect-caused galls are seen for the first time in the Cretaceous, approximately 250 million years later. The intervening years saw the rise and fall of the great coal forests composed of lycopods and horsetails, and an abundance of cycads and gymnosperms, but to our knowledge no insect-caused galls were formed. Thus, the very early history of galls awaits more complete paleobotanical information.

To date and reconstruct evolutionary events is the goal of paleobiologists. The fossil gall record presently indicates a few key events and suggests many more. Our interest in galls and more generally in insect/plant interactions requires that the record be enriched through a broad and thorough search for specimens.

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NOTE

The First Report of an Aphid with Only One Cornicle
(Homoptera: Aphididae)

It is not uncommon to find in a collection of aphids one that has one or both cornicles malformed. The malformation can be minor or it can result in a shortened cornicle or one that does not have an opening to one that is represented by only a very small projection on the dorsum.

Aphids with more than the usual pair of cornicles have been reported by Zirnits (1930. *Fol. Zool. Hydrobiol.* 2: 1-3), Remaudière (1964. *Rev. Path. Veg. Entomol. France* 43: 31-35), Leonard (1967. *Proc. Entomol. Soc. Wash.* 68: 320), Medler and Ghosh (1967. *Proc. Entomol. Soc. Wash.* 69: 366), Kumar and Burkhardt (1971. *J. Kans. Entomol. Soc.* 44(2): 172-181), and Russell (1975. *J. Wash. Acad. Soc.* 65(1): 40-41). Russell (op. cit.) gave a good discussion of the species involved and the placement and form of the usual and additional cornicles. To my knowledge, an aphid with just one cornicle has never been reported in the literature.

In 1984 I received for identification (IIBIII lot number 84 07081) a vial of the aphid *Cinara terminalis* (Gillette and Palmer) collected on June 27, 1984, from pinyon pine [*Pinus edulis* Engelman] at Thoreau, New Mexico, by G. L. Nielsen. In the collection of 100+ aphids, all but one of the adults and all of the immature forms had two fully-developed, normal cornicles. Fig. 1 illustrates on the left a typical apterous adult female with two "normal" cornicles while on the right is the apterous adult female with only one "normal" cornicle on its left side. This



Fig. 1. Apterous adult females of *Cinara terminalis*. Aphid on left has two "normal" cornicles; aphid on right has only one "normal" cornicle.

apterous adult female exhibits all of the typical characteristics of the species except for the noticeable absence of the right cornicle. The whitish patches are internal and disappeared when the aphids were cleared and mounted on slides. When slide-mounted, the one-cornicle aphid had no indication of a second cornicle. This unusual aphid and a few of the "normal" apterous females have been mounted on slides and are deposited in the National Collection of Insects.

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PROC. ENTOMOL. SOC. WASH.
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NOTE

First record in Maryland of *Anomala orientalis* (Waterhouse) (Coleoptera: Scarabaeidae)

On 14 May 1985 larvae tentatively identified as *Anomala orientalis* (Waterhouse) were collected from the root area of Canadian hemlock, *Tsuga canadensis* (L.) Carr., at a commercial nursery in Millington, Kent Co., Maryland. On 13 June 1985 adults were collected from the same plants and identified as *A. orientalis*. A single specimen of *A. orientalis* was also taken at a botanical garden in Wheaton, Montgomery Co., Maryland on 12 June 1985 from *Juniperus* sp. foliage.

The published range of this species is Connecticut, New Jersey, and New York (Potts, 1977. Pan-Pac. Entomol. 53: 34-42). Because both Maryland collections were associated with nursery stock and the hemlocks at Millington came as young plants in soil from New York in 1983, it is likely *A. orientalis* was introduced into Maryland with the plant material. *Anomala orientalis* should be considered established in Maryland. Specimens are deposited in the collections of the Maryland Department of Agriculture, National Museum of Natural History, University of Maryland, and author.

Maryland Department of Agriculture Contribution number 42-85.

C. L. Staines, Jr., *Maryland Department of Agriculture, Office of Plant Industries and Pest Management, Plant Protection Section, 50 Harry S. Truman Parkway, Annapolis, Maryland 21401.*

NOTE

A Search for the Type Series of *Nematocentropus omeiensis* Huang
(Lepidoptera: Neopseustidae)

In 1965 (Acta Zootax. Sin. 2: 33-36) Huang Chi-ling of the Nanking College of Agriculture described a relatively inconspicuous but phylogenetically significant moth from Emeishan [sometimes transliterated Omeishan] in Sichuan Province, Peoples Republic of China (PRC). The syntypic series of this new genus and species, *Nematocentropus omeiensis*, consisted of two specimens (male and female), with no mention of their deposition provided. Obviously uncertain as to the family affinities of this primitive moth, Huang mysteriously placed it in the Mnesarchaeidae, a small hepialoid family endemic to New Zealand, on the basis "of the presence of two spurs on the middle tibia."

Küppers and Speidel (1980. Atalanta 11: 55-65) synonymized *Archepiolus* Mutuura (1971. Can. Entomol. 103: 1129-1136), a genus of Neopseustidae described from Assam, India, under *Nematocentropis*. Their decision was based solely upon the published descriptions of these taxa and not upon the examination of actual specimens. Since 1976, I and a few colleagues suspected this synonymy but were hesitant in proposing it until the formerly inaccessible types of *Nematocentropus* could be studied.

During a visit to the PRC in November 1979 as a member of a delegation of museum specialists from the Smithsonian Institution, I had the opportunity to visit several entomological research centers. In the course of this tour, I was able to trace the present deposition of one of Huang's syntypes and, thus, to confirm the synonymy of the two genera in question.

With the assistance of H. F. Chu, Deputy Director of the Institute of Zoology, Academia Sinica in Beijing, we located one syntype of *N. omeiensis* in their collection under the family Eriocraniidae. Its abdomen was missing and further searching revealed no dissected remains. The published illustrations of both the male and female genitalia of *N. omeiensis* indicate that they were drawn *in situ* without dissection. Because a frenulum is absent in this jugate family, it was not possible to determine the sex of the specimen. The wings of the syntype are almost completely denuded, thus imparting a very dissimilar appearance with the fully scaled holotype of *Archepiolus schmidi* Mutuura. Most likely the two species are distinct, as recognized by Küppers and Speidel, although the genitalia drawings by Huang are nearly unintelligible. Until either the missing male is found or additional specimens collected from the type locality, the specific relationship of these two names will remain questionable. In this connection it is pertinent that a recent attempt to collect additional specimens of *N. omeiensis* was made. Mr. and Mrs. Scott Miller visited Emeishan in 1982 on a collecting trip partially sponsored by the Smithsonian Institution (Miller, 1982. Sphecos, No. 6: 17-18). Although originally told that they would be permitted to collect on Emeishan and equipped with portable UV lights for the occasion, they were not permitted to do so once they reached their destination.

During my 1979 visit I also inquired about the presence of the missing *Ne-*

matocentropus material in Nanjing. I was told that the Nanjing College of Agriculture was at the time undergoing considerable reorganization, and that the entomological collection was unavailable for inspection. I was also informed that Mr. Chi-ling Huang had passed away the previous year. Recent inquiries to the Institute of Zoology in Beijing concerning the discovery of any additional material of *Nematocentropus* or the possibility of borrowing the extant type have produced no results.

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NOTE

An Unusual Food Plant for Adult *Cerotoma trifurcata* (Forster) (Coleoptera: Chrysomelidae)

On 24 May 1985 adult bean leaf beetles (*Cerotoma trifurcata* (Forster); Coleoptera: Chrysomelidae) were observed feeding on the foliage of *Wisteria floribunda* (Willdenow) (Fabaceae) in a commercial nursery in Saint Mary's Co., Maryland. Recorded host plants of *C. trifurcata* are *Lespedeza* spp., *Amphicarpa* sp. (Chittenden, 1892. Proc. Entomol. Soc. Wash 2: 261-267), *Desmodium* spp., *Vigna unguiculata* (L.) Walpers, *Phaseolus* sp. (Chittenden, 1897. USDA Div. Entomol. Bull. 9: 64-71), *Strophostyles helvola* (L.) Elliott, and *Glycine max* (L.) Merrill (Isely, 1930. Ark. Agric. Expt. Stn. Bull. 248). None of the recorded host plants was seen in the nursery. However, adults were not found feeding on two legumes in the nursery: *Cercis canadensis* L. and *Gleditsia triacanthos* L. Both *Cercis* and *Gleditsia* are in the fabaceous subfamily Caesalpinioideae whereas *Wisteria* and the previously recorded host plants are in the subfamily Papilionoideae (Fernald, 1970. *Gray's Manual of Botany*, 8th ed.). The *W. floribunda* plants were in several blocks scattered over a 0.5 ha. area and *C. trifurcata* adults were collected on plants in each block. This is the first feeding record of *C. trifurcata* on a nursery plant.

Maryland Department of Agriculture Contribution number 41-85.

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NOTE

Parasites Reared From Eggs of the Orange Palm Dart,
Cephrenes augiades sperthias (Lepidoptera: Hesperiiidae), in Australia

During my sabbatical leave in Australia in 1984, I collected lepidopterous eggs from wild and cultivated plants to obtain *Trichogramma* for biosystematic studies. While collecting near Palmwoods, Queensland, on May 7, I noted that a rather large, hemispherical, lepidopterous egg commonly occurred on palm fronds and that many of the eggs apparently were parasitized (black). These eggs later were identified as being those of a hesperiid, the orange palm dart, *Cephrenes augiades sperthias* (Felder). Henceforth, orange palm dart eggs were collected in several areas of Queensland and shipped to the Division of Biological Control, University of California, Riverside, where they were held in quarantine until emergence of larvae or adult parasites.

Altogether, six species of hymenopterous parasites, representing five families, were obtained (Table 1). Based on the number of eggs parasitized by each, the most common species were *Ooencyrtus* nr. *shakespearei* (Girault), *Telenomus* sp., *Centrodora australiensis* (Girault) (originally as *Tumidiscapus australiensis* Girault), *Ooencyrtus* sp. nov. nr. *shakespearei* (Girault), *Trichogramma* sp., and *Anastatus* sp., in that order.

The results show that orange palm dart eggs in Queensland, Australia, are a rich source of chalcidoid egg parasites. This would be especially important in-

Table 1. Parasites reared from eggs of the orange palm dart on palm fronds. Queensland, Australia, 1984.

Parasites	Collection	
	Localities	Dates
Aphelinidae:		
<i>Centrodora australiensis</i> (Girault) (orig. as <i>Tumidiscapus australiensis</i> Girault)	Cairns	May 21
Encyrtidae:		
<i>Ooencyrtus</i> nr. <i>shakespearei</i> (Girault)	Cairns	May 10
	Gorkeys Knob	May 12
<i>Ooencyrtus</i> sp. nov. nr. <i>shakespearei</i> (Girault)	Palmwoods	May 7
Eupelmidae:		
<i>Anastatus</i> sp.	Cairns	May 21
	Townsville	May 24
Scelionidae:		
<i>Telenomus</i> sp.	Cairns	May 10
	Gorkeys Knob	May 12
	Port Douglas	May 15
Trichogrammatidae:		
<i>Trichogramma</i> sp.	Townsville	May 25

formation if the hesperiid should ever become an exotic pest (e.g. on ornamental palms in southern California if accidentally introduced here).

I thank the following individuals for identifying the parasites: J. D. Austin, Z. Bouček, and J. S. Noyes, British Museum (Natural History), London, England; and E. R. Oatman and J. D. Pinto, Department of Entomology, University of California, Riverside. I also thank I. Galloway, Department of Primary Industries, Indooroopilly, Brisbane, Australia, for identifying the orange palm dart.

E. R. Oatman, *Division of Biological Control, University of California, Riverside, California 92521.*

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NOTE

Restoration of the Species Name *Salda coriacea* Uhler, 1872 (Hemiptera: Saldidae)

The combination *Salda coriacea* proposed by Uhler (1872. Prelim. Rept. Geol. Surv. Montana, 4: 421) for his new species has been treated as preoccupied by *Salda coriacea* (Fabricius) (1803. Syst. Rhyn., p. 115).

Fabricius' 1803 usage was as a new combination for his *Acanthia coriacea* which he had described in 1776 (Gen. Ins., pp. 299) and cataloged in 1794 (Entomol. Syst., pp. 69). In 1804 it was removed from *Salda* to the combination *Lygaeus coriaceus* by Latreille (Hist. Nat., 12: 220) and then in 1807 to the combination *Capsus coriaceus* by Fallén (Mon. Cim., pp. 98). The latter combination was a forerunner to the eventual placement of the Fabrician species in the family Miridae where it stands today in the combination *Orthocephalus coriaceus* (Fabricius).

Uhler's combination *Salda coriacea* was proposed nearly seventy years after the ephemeral usage by Fabricius and hence at no time was in direct conflict with it. More important, the post-1960 rejection of Uhler's combination as a secondary homonym by Kelton and Lattin (1968, Nat. Can., 95: 664) subjects it to Article 59(d) of the International Code of Zoological Nomenclature (1985, Edit. 3) which directs that if the two species in question are not congeneric the secondary junior homonym is to be restored. Accordingly, *Salda coriacea* Uhler, 1872, is here restored to use and the replacement name *Salda provancheri* Kelton and Lattin is placed in its synonymy as an unnecessary new name (a junior objective synonym) for Uhler's species.

I am grateful to Thomas J. Henry and Curtis W. Sabrosky for reviewing this manuscript.

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NOTE

New Host Record and Range Extension for
Dioryctria abietivorella (Grote)
(Lepidoptera: Pyralidae: Phycitinae)

In 1983, several lepidopterous larvae were found on Fraser's fir, *Abies fraseri* (Pursh) Poir., by a grower of Christmas trees in western North Carolina. One of the larvae was sent to the North Carolina State University Plant Disease and Insect Clinic and identified as *Dioryctria* sp. Later that year, five additional larvae were obtained from the same location, three of which were reared to adults (2 ♂, 1 ♀) and identified as *Dioryctria abietivorella* (Grote).

The larvae were in the last instar when collected in early August and were feeding on small (ca. 1–2 m tall) Fraser's firs growing on a plantation near Bakersville, Mitchell County, North Carolina. They had fed primarily within the terminals of the trees. Silk, frass, and needle fragments provided conspicuous external evidence of the presence of the larvae. The larvae were taken to the laboratory in Raleigh, N.C. and placed on host material collected at Bakersville. Pupation occurred within a cocoon formed at or near the site of injury; adults emerged from the cocoons about three weeks later.

In 1984, on the same plantation, the grower reported a light infestation, presumably of the same species, with larvae present August through late October (Ayers, W., 1984, pers. comm.). We were unable to obtain any of the larvae. No infestation of the plantation occurred in 1985.

Many species of fir, pine, spruce and larch have been listed as hosts of *D. abietivorella* (Hedlin, Yates, Tovar, Ebel, Koerber and Merkel, 1981. Cone and Seed Insects of North American Conifers, p. 78), but Fraser's fir has not been reported previously as a host. Host cones appear to be the favored food of *D. abietivorella* larvae (Hedlin et al., loc. cit., p. 79). There is no clear evidence that *D. abietivorella* feeds in the cones of Fraser's fir, although several undetermined lepidopterous larvae were found in 1984, associated with damaged cones in a Fraser's fir seed orchard in Crossnore, Avery County, North Carolina (Rogers, D., 1985, pers. comm.).

Hedlin et al. (loc. cit., p. 79) included only Virginia and Tennessee as the southernmost range of *D. abietivorella* in the eastern United States. It is apparent that small populations of *D. abietivorella* also occur in western North Carolina.

We thank D. L. Stephan of the North Carolina State University Plant Disease and Insect Clinic, for bringing the initial *Dioryctria* larvae to our attention, and W. Ayers for access to his land, and assistance in collecting larvae. Adults and associated larvae of *D. abietivorella* have been deposited in the North Carolina State University Insect Collection (NCSU).

This is paper No. 10186 of the Journal Series of the North Carolina Agricultural Research Service, Raleigh, N.C. 27695-7601.

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BOOK NOTICE

Directory of Systematists. Anonymous. Entomological Society of America. 110 pp. No date, no price.

This little volume consists of a 91-page list of entomologists, with their interests ("ecology, anatomy," etc.). There follow six lists of names only, Behavior, Curator, Fossils, Morphology, Systematics, and Taxonomy. The first list includes addresses and telephone numbers. The Introduction says the lists come from the Entomological Society of America's member data files, accurate to April 1, 1985; the Introduction contains a grammatical error, perhaps slipped in to call attention to that date.

It is difficult to know for what audience this book is intended. A directory of taxonomists offers very little if it lacks (as this one does) any cross-referencing by taxonomic group; the same is true of a list of students of behavior. True, the address-list provides the interests of most people, but this serves little purpose. First, many people are listed merely as "Section A," with no explanation of what "Section A" means. Second, the address-list is titled "Systematists," thus appearing to exclude some morphologists and all students of behavior. And third, of course, one must know the individual before one can look him/her up to learn his/her interest; but usually one knows the interest if one knows the individual.

Further, the phrase "Section A" has meaning only for members of the Entomological Society of America. Yet these members have a copy of the ESA's membership list, which includes all the people in this Directory, plus many more, and is free to members. The mystery remains: for whom was this book intended?

There is the further mystery of the book's provenance. Although "Entomological Society of America" appears on the cover, the book was not approved (as all special ESA publications must be) by that Society's Publications Council. One wonders if this is a pirate or bootleg production, slipped surreptitiously from the computer some stillly night. If so, will the Society call it back, and will it—like the first edition of Robert Graves's autobiography—command enormous prices in the auction rooms of Sotheby, Christie, and Swann?

I cannot recommend this book to ESA members, who have their membership list; I cannot recommend it to nonmembers, who will not know what "Section A" means; and I cannot recommend it to members or nonmembers, for it is merely a list of people without a cross-referencing key for access.

Carl W. Schaefer, *Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06268.*

SOCIETY MEETINGS

915th Regular Meeting—June 6, 1985

The annual banquet of the Entomological Society of Washington and the Pest Science Society of Washington was held on June 6, 1985, in the solar-powered Intercultural Center Galleria on the Georgetown University campus, Washington, D.C. The banquet chairman and master of ceremonies was Edward M. Barrows. After a social hour, dinner began at 7:30 p.m. After dinner, guests at the head table and past presidents were introduced. Professor Barrows then gave a short history of Georgetown University from its founding in 1789 to the present. The guest speaker was Suzanne W. T. Batra, Agricultural Research Service, U.S. Department of Agriculture, Beltsville, Maryland, who spoke on deceit in nature. Various forms of mimicry were described. Much of Dr. Batra's talk focused on "mummy-berry disease," a fungus that causes blueberry leaves to wilt and develop a flower-like appearance, secrete sugars, and become fragrant. Insect pollinators are attracted to these flower-like leaves, ingest the sugar, and transmit conidia to the flowers of the host, thus spreading the infection. The banquet was attended by 92 persons. Table centerpieces were provided by Edward M. Barrows.

Thomas E. Wallenmaier, *Recording Secretary*.

916th Regular Meeting—October 3, 1985

The 916th Regular Meeting of the Entomological Society of Washington was called to order by President Donald M. Anderson in the Naturalist Center, National Museum of Natural History, at 8 p.m. on October 3, 1985. Twenty-eight members and thirteen guests were present. Minutes of the two previous meetings were read and approved. R. G. Robbins read the names of the following applicants for membership: Suzanne W. T. Batra, Agricultural Research Service, Beltsville East, USDA-ARS, Beltsville, MD 20785; Jack R. Davis, 11306 Eubank, Austin, TX 78758; Ralph W. Holzenthal, Department of Entomology, Clemson University, Clemson, SC; Ellen M. Thoms, Department of Entomology, VPI&SU, Blacksburg, VA; John H. Werren, Department of Entomology, University of Maryland.

The president announced the appointment of an auditing committee consisting of J. Kingsolver, J. Neal, and D. Smith, Chairman. A nominating committee was also appointed consisting of F. Thompson, J. Aldrich, and D. Davis, Chairman. T. Bissell exhibited some twigs girdled by a local cerambycid beetle.

The speaker for the evening was Warren Steiner, Department of Entomology, National Museum of Natural History, Washington, D.C. His talk was entitled "Mountain of the Mist: An Entomologist's View of Cerro De La Neblina, Venezuela." A multinational expedition involving Smithsonian scientists, in cooperation with the Foundation of Physics, Mathematics, and Natural Sciences of Venezuela, visited a remote area of Venezuela during January to March 1985. After travelling by plane, boat, and helicopter, the party reached their base camp. Mr. Steiner concentrated on collecting water beetles. Fifty-five thousand insect

specimens were collected on the trip, half of which will be identified and returned to Venezuela scientists. Slides were shown of some of the insects encountered, including a giant pink larva in the moth family Megalopygidae. Various scientific disciplines were represented on the expedition including botanists and ornithologists. Specimens in many new genera and species were collected, and a wide variety of vegetation types were encountered. In one incident some members ate blueberries which turned out to be highly toxic.

One international visitor was introduced at the close of the meeting: John Leader, a biophysicist from the University of Otago, New Zealand. The meeting was adjourned at 9:30 p.m. after which refreshments were served.

Thomas E. Wallenmaier, *Recording Secretary*.

917th Regular Meeting—November 7, 1985

The 917th Regular Meeting of the Entomological Society of Washington was called to order by President Donald M. Anderson in the Naturalist Center, National Museum of Natural History, at 8 p.m. on December 7, 1985. Twenty-five members and eleven guests were present. Minutes of the previous meeting were read and approved with two minor corrections. Membership Chairman, G. B. White, read the names of the following applicants for membership: Gregory W. Courtney, Department of Entomology, University of Alberta, Edmonton, Alberta; D. L. Deonier, Department of Zoology, Miami University, Oxford, OH; Paul Hanson, Department of Entomology, Oregon State University, Corvallis, OR; R. W. Longair, Department of Environmental Biology, University of Guelph, Guelph, Ontario; W. A. Palmer, 2714 Pecan Drive, Temple, TX; and E. R. Easton, Plant Sciences Department, South Dakota State University, Brookings, SD.

The nominating committee reported the following slate of nominees: President-elect, T. E. Wallenmaier; Recording Secretary, P. M. Marsh; Corresponding Secretary, R. G. Robbins; Treasurer, N. E. Woodley; Program Chairman, M. J. Raupp; Membership Chairman, G. B. White; Custodian, V. L. Blackburn; and Editor, R. J. Gagné. Paul Spangler exhibited a copy of Volume II of "The Coleoptera of Japan in Color" by S. Ueno, Y. Kurosawa, and M. Sato, published in 1985. Mrs. Spangler showed a copy of an interesting children's book entitled "Trouble in Bugland, A Collection of Inspector Mantis Stories" by W. Katzwinkle. E. Barrows showed two lovely calendars, one sold by the Entomological Society of America and the other by an endangered wildflower group.

The speakers for the evening were Drs. John and Jenny Leader of the University of Otago, Dunedin, New Zealand. Their talk was entitled "New Zealand and its Entomology." They first discussed the geography, flora, and fauna of New Zealand. Slides of a wide range of natural habitats were shown covering both North Island and South Island. They gave details on the Entomological Society of New Zealand, on various systematic activities in New Zealand, on the professional role of entomologists in agriculture and forestry, and on the academic role of entomologists in New Zealand. Federal employment of entomologists is done by the Department of Scientific and Industrial Research, which employs 10 entomologists. There are few entomologists in academic positions. The remainder of the talk was devoted

to a synopsis of the fauna of New Zealand. After discussing some of the mammals which now live in New Zealand, a survey of the insects of New Zealand was given. There are only six species of butterflies, although other Lepidoptera such as the primitive Micropterigidae are abundant. Trichoptera that live in saltwater tidal ponds, ephydrid flies that live on small algal mats in hot springs, and a species of Orthoptera, *Hemideina maori*, which is about the size of a rat, were some of the more interesting insects discussed.

One international visitor was introduced, Edward Becker, from Canada. The meeting was adjourned at 9:45 p.m. after which refreshments were served.

Thomas E. Wallenmaier, *Recording Secretary*.

918th Regular Meeting—December 5, 1985

The 918th Regular Meeting of the Entomological Society of Washington was called to order by President Donald M. Anderson in the Naturalist Center, National Museum of Natural History, at 8 p.m. on December 5, 1985. Nineteen members and eight guests were present. Minutes of the previous meeting were read and approved. Membership Chairman, G. B. White, read the names of the following applicants for membership: G. A. Hoover, R.D. #4, Box 171, Halifax, Pennsylvania, and M. D. Schwartz, Department of Entomology, American Museum of Natural History, New York, New York. Mr. White also reported that there were 26 new members for the year.

The annual treasurer's report (published in this Proceedings issue under Reports of Society Officers) was given by F. C. Thompson in the absence of T. J. Henry. Dr. Thompson noted that again this year the Society had spent more than it had taken in. The annual Editor's report was given by R. J. Gagné.

The nominating committee presented its slate of nominees for Society offices and asked for any additional nominations from the floor. It was moved by D. R. Davis and seconded by E. Barrows that the proposed slate of nominees be accepted as new officers. The motion passed unanimously.

The speaker for the evening was Brian D. Farrell, Department of Entomology, University of Maryland, College Park, Maryland. His talk was entitled, "Coevolution and Natural History: Chrysomelids and Bitter Mints." *Phyllobrotica* species feeding on members of the mint family, Labiatae, were studied to shed light on the question of whether herbivorous insects coevolved with their host plants. The distribution of *Phyllobrotica* species was compared with the distribution of mint plants to determine host specificity. Laboratory studies were also performed. Part of the research also involved determining the phylogeny of the genus *Phyllobrotica*. The talk was followed by questions from the audience.

D. M. Anderson acknowledged the gratitude of the Society for the work of Helen Sollers-Riedel as Chairman of the Hospitality Committee. The new Hospitality Committee consists of Margaret Collins, Mignon Davis, and David Nickle. Dr. Anderson also thanked all the officers of the Society for their efforts in 1985. He passed the gavel to the new president, E. M. Barrows, who adjourned the meeting.

Thomas E. Wallenmaier, *Recording Secretary*.

REPORTS OF SOCIETY OFFICERS FOR 1985

TREASURER
(1 November 1984 to 31 October 1985)

Summary	General Fund	Special Publication Fund	Totals
On Hand, 1 November 1984	30,766.19	51,383.29	82,149.48
Total Receipts	56,381.41	8,718.34	65,099.75
Total Disbursements	65,911.84		65,911.84
On Hand, 31 October 1985	21,235.76	60,101.63	81,337.39

Thomas J. Henry, *Treasurer*

EDITOR

The Society published 913 pages in 1985, remarkable when one considers we budget for 800 pages! I gratefully acknowledge the many manuscript reviewers for their good help and the Publications Committee members for their advice and support.

Our Society acts in some ways as a local organization. As examples, we hold regular meetings for the local Washington area membership and our officers are all local members. But the *Proceedings* is not intended to be a local journal and publishes on any entomological topic exclusive of chemical control. A few correspondents, however, apparently consider the scope to be fairly restricted. During the past year a prospective author wrote that he hoped his manuscript would be favorably considered even though it did not concern systematics. Another was concerned that the scope of the *Proceedings* was too local to allow consideration of his manuscript, which treated western U.S. insects. I made a casual survey of the 102 regular articles (not including notes) that were published in the 1985 volume of the *Proceedings* to see whether the *Proceedings* published only or mainly systematics and treated the local fauna particularly.

Seventy papers chiefly covered systematics or morphology, 28 dealt primarily with other subjects, and 4 were about half systematics and half biology. Seventy papers treated insects from North America including Mexico (insects, entomologists, and many other people do not consider the border between U.S. and Mexico a natural barrier); 16, Central and South America; 4, Western Hemisphere; 3, Afrotropical; 3, palearctic, 1, holarctic, and 5, oriental, Pacific, and Australian. Approximately as many papers treated western U.S. insects as eastern, but this did not break down easily.

The broad subject matter of the latest volume of the journal depended on the 123 individuals who authored or coauthored the 102 articles (some authors authored more than 1 paper but are counted only once here). Twenty-two of them were from the Washington, D.C., metropolitan area, 80 from elsewhere in the U.S., and 21 were from outside U.S. (including U.S. citizens living abroad). Twenty-eight articles concerned Diptera, 15 Lepidoptera, 13 Hymenoptera, 12

Coleoptera, 7 Homoptera, 6 Hemiptera, 5 Ephemeroptera, and no more than 3 of the remaining 16 articles on any particular order. In other years, also, the Society published a preponderance of Diptera articles, which caused one of my colleagues to remark that the Proceedings was a Diptera journal. One possible reason for the great number of Diptera papers is that, unlike coleopterists and lepidopterists, dipterists do not have their own particular subject journal.

This casual survey of one volume's articles indicates that the Proceedings has a broad and varied subject matter. This happens without active effort expended on searching out articles. Generally, the papers published reflect what is submitted: If a manuscript is good (as determined by the reviewers), not overlong, and not on insect control, it is publishable. The mix of a volume reflects in large part the Society's membership.

Raymond J. Gagné, *Editor*.

MEMBERSHIP LIST OF THE
ENTOMOLOGICAL SOCIETY OF WASHINGTON

1 February 1986

Articles III (Section 7) and V (Section 5) of the Bylaws of the Entomological Society of Washington direct the Corresponding Secretary to publish a membership list at least once every three years. Accordingly, it is my pleasure to present the following roll and to announce that our total membership now stands at 632. Members currently reside or receive the *Proceedings* in 48 states of the United States (the exceptions: Alaska and Arkansas) as well as the Commonwealth of Puerto Rico. Leading jurisdictions are Maryland (109 members), District of Columbia (66), California (49), Virginia (33), and Florida (28). In addition, 61 members are either foreign nationals or Americans living in one of 23 countries abroad. Of these, Canada is by far the best represented with 20 members. Other regions are Latin America (6 countries, 15 members, 5 of them in Mexico), Europe (8 countries, 14 members), Asia (4 countries, 6 members), Africa (3 countries, 3 members), and Australia (3 members). Major nations noteworthy by their absence are the People's Republic of China and the USSR.

In the present list names of Honorary Members are capitalized, names of Emeritus Members are italicized, and Life Members are distinguished by an asterisk (*) alongside the dates on which they joined the Society. Dates of election to Honorary or Emeritus status appear in parentheses. In this regard, Mr. C. F. W. Muesebeck enjoys the unique distinction of having been elected Honorary President in 1970.

I thank Mrs. Dianne Mathis for her painstaking assistance in the preparation of this list, but all errors of omission or commission (there are bound to be several) are entirely my own. Corrections may be mailed to me at the address on the inside front cover of this issue, or call during regular business hours, E.S.T., at (301) 423-5693. All changes brought to my attention will be read at regular meetings of the Society and published in the *Proceedings* by the Recording Secretary.

Richard G. Robbins, *Corresponding Secretary*.

Abercrombie, J. 1975 Maryland
Adams, J. R. 1963 Maryland
Adams, M. S. 1983 New York
Adamski, D. 1984 Mississippi
Addington, R. J. 1964 District of Columbia
Adler, V. E. 1961 Maryland
Agafitei, N. J. 1981 Illinois
Aitken, T. H. G. 1957 (1984) Connecticut
Aldrich, J. R. 1983 Maryland
Altman, R. M. 1964 Maryland
Anderson, D. M. 1954 District of Columbia
Anderson, J. J. 1984 Maryland
Anderson, L. D. 1944 California
Anderson, W. H. 1937 Maryland

App, B. A. 1952 Florida
Appel, A. G. 1983 Alabama
Arduser, M. S. 1985 Missouri
Armitage, B. J. 1983 Alabama
Arnaud, P. H. 1955 California
Arnett, R. H., Jr. 1980 Florida
Ashlock, P. D. 1958 Kansas
Austin, D. F. 1977 Florida
Bacon, N. 1982 Pennsylvania
Baker, E. W. 1944 Maryland
Ball, G. E. 1948 CANADA
Barber, K. N. 1985 CANADA
Barnes, J. K. 1979 New York
Barnett, D. E. 1976 Maryland

- Barnum, A. 1956 Utah
 Barr, A. R. 1951 California
 Barr, W. F. 1948 Idaho
 Barrows, E. M. 1976 District of Columbia
 Batra, S. W. T. 1985 Maryland
 Baumann, R. W. 1973 Utah
 Beal, R. S., Jr. 1958 Arizona
 Bechtel, R. C. 1960 Nevada
 Beck, T. R. 1979 Maryland
 Becker, E. C. 1951 CANADA
 Beckham, C. A. 1983 Maryland
 Bell, R. T. 1955 Vermont
 Bellinger, R. G. 1972 Virginia
 Berg, C. O. 1975 New York
 Bergman, P. W. 1966 Virginia
 Berry, R. L. 1972 Ohio
 Bezark, L. G. 1974 California
 Bicha, W. 1981 Ohio
 Bickel, D. J. 1981 Massachusetts
 Bickley, W. E. 1949* Maryland
 BISSELL, T. L. 1941 (1983) Maryland
 Blackburn, V. L. 1984 Maryland
 Blanchard, A. 1968 Texas
 Boese, J. L. 1977 District of Columbia
 Boesel, M. W. 1973 Ohio
 Boettcher, R. A. 1955 District of Columbia
 Bohart, R. M. 1944 California
 Bohnsack, K. K. 1958 California
 Bouseman, J. K. 1975 Illinois
 Bowen, T. W. 1980 North Carolina
 Brajkovic, M. 1984 YUGOSLAVIA
 Brassard, D. W. 1978 Virginia
 Brigham, W. U. 1975 Illinois
 Brou, V. A. 1985 Louisiana
 Brown, B. V. 1982 CANADA
 Brown, F. M. 1975 Colorado
 Brown, H. P. 1977 Oklahoma
 Brown, R. 1985 Florida
 Brown, R. L. 1979 Mississippi
 Bueno-Soria, J. 1977 MEXICO
 Burditt, A. K., Jr. 1965 Washington
 Burger, J. F. 1973 New Hampshire
 Burke, H. R. 1981 Texas
 Burks, B. D. 1938 Arizona
 Burnett, J. A. 1975 California
 Burns, J. M. 1975 District of Columbia
 Burrows, W. L. 1983 West Virginia
 Bushman, D. W. 1983 Maryland
 Butler, L. 1966 West Virginia
 Byers, G. W. 1984 Kansas
 Calabrese, D. M. 1980 Pennsylvania
 Campbell, J. M. 1966 CANADA
 Carlson, R. W. 1970* Maryland
 Carpenter, J. M. 1984 Massachusetts
 Carroll, J. F. 1977 Maryland
 Casdorff, D. G. 1977 California
 Cave, R. 1977 Alabama
 Chapin, J. B. 1973 Louisiana
 Charpentier, P. O. 1962 Connecticut
 Chilson, L. M. 1977 Maryland
 Chittick, H. A. 1946 New York
 Clark, S. T. 1981 Texas
 Clark, W. E. 1975 Alabama
 Clarke, J. F. G. 1936 District of Columbia
 Cochran, D. G. 1981 Virginia
 Coddington, J. 1984 District of Columbia
 Coffman, C. C. 1980 West Virginia
 Cohen, N. Y. 1983 Maryland
 Connell, J. G. 1974 New York
 Cook, D. R. 1952 Michigan
 Cooper, C. M. 1976 Mississippi
 Cooper, K. W. 1955 California
 Copeland, T. P. 1977 Tennessee
 Cornell, C. F. 1984 Virginia
 Corpus, L. D. 1985 Kansas
 Coulson, J. R. 1961 Maryland
 Courtney, G. W. 1985 CANADA
 Covell, C. V. 1971 Kentucky
 Cowan, D. P. 1984 Michigan
 Craig, G. B. 1954 Indiana
 Crooks, E. E. 1964 Maryland
 Cross, H. F. 1954 Georgia
 Ćurčić, B. P. M. 1982 YUGOSLAVIA
 Currado, I. 1978 ITALY
 Darling, D. C. 1981 CANADA
 Darsie, R. F., Jr. 1949 South Carolina
 Daum, R. J. 1969 Maryland
 Davidson, J. A. 1957 Maryland
 Davis, D. R. 1961 District of Columbia
 Davis, E. J. 1982 Maryland
 Davis, J. R. 1985 Texas
 Davis, L. G. 1952 Virginia
 Davis, M. M. 1979 District of Columbia
 Deeming, J. C. 1974* UNITED KINGDOM
 Deitz, L. L. 1982 North Carolina
 Denning, D. G. 1966 California
 Dennis, S. 1976 Colorado
 Deonier, D. L. 1985 Ohio
 Deyrup, M. A. 1979 Florida
 Dicke, F. F. 1933 Iowa
 Donley, D. E. 1955 Pennsylvania
 Donnelly, T. W. 1962 New York
 Doria, J. J. 1977 Virginia
 Dos Passos, C. F. 1947 New Jersey
 Downes, W. G. 1981 Connecticut
 Downes, W. L. 1985 Michigan
 Doyen, J. T. 1983 California
 Dozier, H. L. 1952* South Carolina
 Drea, J. J. 1984 Maryland
 Drummond, R. O. 1954 Texas
 Duckworth, W. D. 1961 Hawaii
 Duffield, R. 1978 District of Columbia
 Easton, E. R. 1985 South Dakota
 Edmunds, G. F., Jr. 1951 Utah

- Eikenbary, R. D. 1979 Oklahoma
 Elias, M. K. 1972 Maryland
 Emerson, K. C. 1952 Florida
 Emsley, M. G. 1970 Virginia
 Enns, W. R. 1960 Missouri
 Erwin, N. 1986 Maryland
 Erwin, T. L. 1972 District of Columbia
 Evans, E. W. 1984 Kansas
 Evans, H. E. 1948 Colorado
 Evans, W. G. 1957 CANADA
 Evenhuis, N. L. 1980 Hawaii
 Fairchild, G. B. 1939 Florida
 Fales, J. H. 1944 Maryland
 Faran, M. E. 1977 Texas
 Farrell, B. D. 1984 Maryland
 Farrier, M. H. 1984 North Carolina
 Fedde, G. 1962 North Carolina
 Fee, F. D. 1983 Pennsylvania
 Fennah, R. G. 1941 UNITED KINGDOM
 Ferguson, D. C. 1969 District of Columbia
 Fisher, E. M. 1977 California
 Fisk, F. W. 1968 Florida
 Flechtmann, C. 1968 BRAZIL
 Flint, O. S., Jr. 1961 District of Columbia
 Fluno, J. A. 1957 Florida
 Foote, B. A. 1958 Ohio
 Foote, R. H. 1950 Virginia
 Forattini, O. P. 1956 BRAZIL
 Foster, J. R. 1953 Maryland
 Fox, I. 1936 Puerto Rico
 Franclemont, J. G. 1947 New York
 Freeman, J. V. 1981 Vermont
 Freidberg, A. 1979 ISRAEL
 Freytag, P. H. 1979 Kentucky
 Froeschner, R. C. 1961 District of Columbia
 Gagné, R. J. 1966* District of Columbia
 Gentry, J. W. 1958 Florida
 Gerberg, E. J. 1953 Maryland
 Gerberich, A. G. 1981 District of Columbia
 Ghorpade, K. D. 1983 INDIA
 Gibson, E. H. 1916 (1965) Texas
 Gibson, L. P. 1981 Ohio
 Giles, F. E. 1981 Maryland
 Gill, G. D. 1958 Michigan
 Gimpel, W. F., Jr. 1970 Maryland
 Glick, J. I. 1979 North Carolina
 Godfrey, G. L. 1971 Illinois
 Goeden, R. D. 1982 California
 Gonzalez, R. H. 1974 CHILE
 Gordh, G. 1975 California
 Gordon, R. D. 1968 District of Columbia
 Gorham, J. R. 1974 District of Columbia
 Gotwald, W. H., Jr. 1977 New York
 Grabowski, W. B. 1970 New Mexico
 Gregg, R. E. 1945 Colorado
 Grimaldi, D. A. 1984 New York
 Grissell, E. E. 1979 District of Columbia
 Grogan, W. L., Jr. 1974 Maryland
 Grothaus, R. H. 1981 Wisconsin
 Gunther, R. G. 1981 Illinois
 GURNEY, A. B. 1936 (1979) District of Columbia
 Habeck, D. H. 1957 Florida
 Hacker, J. D. 1971 West Virginia
 Hagen, K. S. 1949 California
 Haines, K. A. 1952 Virginia
 Halstead, J. A. 1983 California
 Hamid, A. 1976 NIGERIA
 Hamilton, S. W. 1982 South Carolina
 Hamman, R. E. 1968 District of Columbia
 Hannemann, H.-J. 1979 EAST GERMANY
 Hanson, P. 1985 Oregon
 Hansson, C. 1985 SWEDEN
 Harbach, R. E. 1972 District of Columbia
 Hardy, A. R. 1974 California
 Harman, D. M. 1966 Maryland
 Harmston, F. C. 1940 Utah
 Harper, P. P. 1977 CANADA
 Harris, S. C. 1979 Alabama
 Harrison, B. A. 1976 District of Columbia
 Harrison, S. J. 1985 Maryland
 Haskins, C. P. 1945 District of Columbia
 Hawkins, B. A. 1983 UNITED KINGDOM
 Hayes, D. K. 1970 Maryland
 Heitzman, R. L. 1980 District of Columbia
 Hendricks, P. 1984 Washington
 Hendrickson, R. M., Jr. 1978 Delaware
 Henry, C. S. 1975 Connecticut
 Henry, R. L. 1984 Indiana
 Henry, T. J. 1975 District of Columbia
 Heppner, J. B. 1974 Florida
 Herman, L. H., Jr. 1965 New York
 Hespeneheide, H. A., III 1981 California
 Hevel, G. F. 1970 District of Columbia
 Hodges, R. W. 1960 District of Columbia
 Hoebeke, E. R. 1980 New York
 Hoffmann, C. H. 1945 Maryland
 Hoffmann, W. E. 1944 Kansas
 Holzbach, J. E. 1983 Ohio
 Holzenthal, R. W. 1985 South Carolina
 Hoogstraal, H. 1946 EGYPT
 Hooker, M. E. 1984 District of Columbia
 Hoover, G. A. 1985 Pennsylvania
 Hopla, C. E. 1961 Oklahoma
 Hopper, H. P. 1978 District of Columbia
 Horne, J. E. 1971 Maryland
 Howden, H. F. 1948 CANADA
 Huang, Y.-M. 1968 District of Columbia
 Hubbard, M. D. 1976 Florida
 Hudson, B. N. A. 1980 CANADA
 Hull, W. B. 1949 Maryland
 Hung, A. C. F. 1981 Maryland
 Huryn, A. D. 1984 Georgia
 Husband, R. W. 1973 Michigan

- Imai, E. M. 1983 Maryland
 Ingles, R. 1975 Puerto Rico
 Irwin, M. E. 1976 Illinois
 Ivie, M. A. 1981 Ohio
 Jackson, D. L. 1966 Ohio
 Jakob, W. L. 1977 Colorado
James, M. T. 1942 (1972) Washington
 Johnson, M. D. 1973 Indiana
 Johnson, N. F. 1980 New York
 Johnson, P. J. 1984 Idaho
 Johnson, P. T. 1951 Maryland
 Jones, R. H. 1955 Colorado
 Jones, S. R. 1985 Pennsylvania
 Joseph, S. R. 1957 Maryland
 Kaster, C. H. 1979 Michigan
 Keirans, J. E. 1984 District of Columbia
 Kelley, R. W. 1982 South Carolina
 Kennedy, J. H. 1977 Pennsylvania
 Kethley, J. B. 1974 Illinois
 Kim, K. C. 1983 Pennsylvania
 King, C. S. 1983 New York
 Kingsolver, J. M. 1963 District of Columbia
 Kirchner, R. F. 1981 West Virginia
 Kissinger, D. G. 1955 California
 Kitayama, C. 1974 California
 Kiteley, E. J. 1971 CANADA
 Kittle, P. 1975 Alabama
 Kliewer, J. W. 1983 Virginia
 Klun, J. A. 1985 Maryland
Knipling, E. F. 1946 (1985) Maryland
 Knisley, C. B. 1981 Virginia
 Knodel, J. J. 1984 New York
Knowlton, G. F. 1935 (1973) Utah
 Knudson, E. C. 1982 Texas
 Knutson, L. V. 1963* District of Columbia
 Kormilev, N. A. 1941 Florida
 Korytkowski, C. A. 1982 PANAMA
 Kosztarab, M. 1978 Virginia
 Krafur, E. S. 1968 Iowa
 Kramer, J. P. 1957 District of Columbia
 Krause, C. R. 1983 Ohio
 Krombein, K. V. 1941* District of Columbia
 Kurczewski, F. E. 1970 New York
 Lager, T. M. 1976 Wisconsin
 Lago, P. K. 1984 Mississippi
 LaGoy, P. K. 1983 Virginia
 Lamb, N. J. 1978 New York
 Lambdin, P. L. 1974 Tennessee
 Lampert, L. L., Jr. 1976 North Carolina
 Langford, G. S. 1924 Maryland
 Larew, H. G. 1982 Maryland
 LaSalle, J. 1982 California
 Lassmann, G. W. 1946 MEXICO
 Latorre, L. T. 1984 West Virginia
 Lavigne, R. 1973 Wyoming
 Leader, J. P. 1986 Maryland
 Levesque, C. 1985 CANADA
 Lewis, P. A. 1974 Ohio
 Lewis, R. E. 1958 Iowa
 Lien, J. C. 1967 REPUBLIC OF CHINA
 Linam, J. 1962 Colorado
 Linkfield, R. L. 1959 New Jersey
 Lipes, J. E. 1974 Maryland
 Longair, R. W. 1985 CANADA
 Louton, J. A. 1982 District of Columbia
 Lowry, J. E. 1983 Maryland
 Ludvik, G. F. 1978 Virginia
 Lund, H. O. 1952 Georgia
 Lyon, R. J. 1961 California
 Mabry, J. E. 1954 Florida
 MacDonald, J. F. 1984 Indiana
 MacKay, W. P. 1982 New Mexico
 Magner, J. M. 1953 Missouri
 Maier, C. T. 1976 Connecticut
 Main, A. J., Jr. 1965 Connecticut
 Maldonado-Capriles, J. 1947 Puerto Rico
 Mallack, J. 1957 Maryland
 Mangan, R. L. 1977 Texas
 Manglitz, G. R. 1956 Nebraska
 Manley, D. G. 1984 South Carolina
 Manuel, K. L. 1983 North Carolina
 Mari Mutt, J. A. 1976 Puerto Rico
 Marsh, P. M. 1960 District of Columbia
 Marshall, S. 1982 CANADA
 Masner, L. 1969 CANADA
Mason, H. C. 1949 (1973) Maryland
 Mason, P. 1984 CANADA
 Mason, T. L., Jr. 1977 West Virginia
 Mason, W. R. M. 1970 CANADA
 Mathieu-Veillard, J. M. 1982 MEXICO
 Mathis, W. N. 1976 District of Columbia
 Matta, J. 1978 Virginia
 Mayor, A. J. 1981 Wisconsin
 McCabe, T. L. 1977 New York
 McCafferty, W. P. 1968 Indiana
 McComb, C. W. 1956 Virginia
 McDaniel, B. 1964 South Dakota
 McDonald, F. J. D. 1983 AUSTRALIA
 McFadden, M. W. 1956 Virginia
McGovran, E. R. 1937 (1973) Maryland
McGuire, J. U., Jr. 1954 (1980) Puerto Rico
 McMurty, J. A. 1981 California
 McPherson, J. E. 1985 Illinois
 Mead, F. W. 1976 Florida
 Mendez, E. 1976 Florida
 Menke, A. S. 1969 District of Columbia
 Menn, J. J. 1985 Maryland
 Messersmith, D. H. 1965 Maryland
 Miller, C. E. 1981 Maryland
 Miller, D. R. 1969 Maryland
 Miller, G. L. 1981 Alabama
 Miller, R. M. 1974 SOUTH AFRICA
 Miller, R. S. 1981 California
 Miller, S. E. 1980 District of Columbia

- Miller, W. E. 1983 Minnesota
 Mitchell, R. T. 1949 (1978) Maryland
 Mockford, E. L. 1955 Illinois
 Mollet, J. A. 1984 California
 Moore, T. E. 1950 Michigan
 Moraes, A. P. A. de 1978 California
 Moran, N. 1982 Michigan
 Morgan, N. O. 1969 Maryland
 Moron, M. A. 1985 MEXICO
 Morse, J. C. 1976 South Carolina
 Moser, J. C. 1973 Louisiana
 MUESEBECK, C. F. W. 1920 (1955) New York
 Mullens, B. A. 1979 California
 Munson, S. C. 1938 (1976) Maryland
 Munte, S. T. 1983 District of Columbia
 Murdoch, W. P. 1966 Pennsylvania
 Murphy, W. L. 1983 Maryland
 Nakahara, S. 1968 Maryland
 Neal, J. W., Jr. 1982 Maryland
 Neff, S. E. 1969 Pennsylvania
 Nelson, C. H. 1969 Tennessee
 Nelson, G. H. 1949 California
 Nelson, R. H. 1933 Pennsylvania
 Neunzig, H. H. 1956 North Carolina
 Newkirk, R. A. 1968 Maryland
 Ng, Y.-S. 1986 Virginia
 Nichols, S. W. 1985 New York
 Nickle, D. A. 1980 District of Columbia
 Nielsen, G. R. 1983 Vermont
 Norden, B. B. 1984 Maryland
 Norrbom, A. L. 1983 District of Columbia
 Norton, R. A. 1978 New York
 Nuhn, T. P. 1981 Virginia
 Nutting, W. H. 1973 California
 Oatman, E. R. 1980 California
 O'Brien, M. F. 1979 New York
 Oman, P. W. 1930 Oregon
 Orth, R. E. 1981 California
 Osbrink, W. L. A. 1984 California
 Osgood, E. A. 1977 Maine
 Pagac, B. B., Jr. 1984 Maryland
 Paggi, A. C. 1984 ARGENTINA
 Pakaluk, J. 1981 Kansas
 Palacios-Vargas, J. G. 1980 MEXICO
 Palmer, W. A. 1985 Texas
 Parker, C. R. 1977 Virginia
 Parker, H. L. before 1918 (1963) FRANCE
 Parrish, D. W. 1963 Maryland
 Parsons, M. 1963 Ohio
 Pena-G., L. E. 1980 CHILE
 Penny, N. D. 1982 California
 Peters, T. M. 1979 Massachusetts
 Peters, W. L. 1971 Florida
 Petersen, J. L. 1981 Florida
 Peterson, R. V. 1952 District of Columbia
 Peyton, E. L. 1968 District of Columbia
 Phillips, S. A. 1985 Texas
 Phillips, W. G. 1955 Maryland
 Pinto, J. D. 1982 California
 Pitkin, B. R. 1977 UNITED KINGDOM
 Plakidas, J. D. 1986 Maryland
 Platt, A. P. 1985 Maryland
 Pogue, M. G. 1980 Minnesota
 Polhemus, J. T. 1964 Colorado
 POOS, F. W. 1923 (1966) Virginia
 Porter, C. H. 1984 Georgia
 Powell, J. E. 1985 Mississippi
 Poyner, M. M. 1969 Maryland
 Pratt, G. K. 1974 Florida
 Pratt, H. D. 1943 Georgia
 Price, R. D. 1963 Minnesota
 Pulawski, W. J. 1975 California
 Rack, G. 1975 WEST GERMANY
 Radovic, I. 1981 YUGOSLAVIA
 Rainwater, C. F. 1954 (1975) Maryland
 Rainwater, H. I. 1964 (1983) Maryland
 Ramos, J. A. 1947 Puerto Rico
 Ramsay, M. J. 1968 Maryland
 Ratcliffe, B. C. 1984 Nebraska
 Raupp, M. J. 1982 Maryland
 Rawlins, J. E. 1974 Pennsylvania
 Reed, W. D. 1931 District of Columbia
 Reichart, C. V. 1946 Rhode Island
 Richardson, H. H. 1939 (1976) New Jersey
 Riegel, G. T. 1952 Illinois
 Riley, D. R. 1984 Texas
 Robbins, R. G. 1979 Virginia
 Roberts, D. R. 1968 Maryland
 Robinson, H. 1963 District of Columbia
 Robinson, W. H. 1975 Virginia
 Rock, E. 1984 Ohio
 Roemhild, G. 1984 Montana
 Rolston, L. H. 1973 Louisiana
 Root, R. B. 1984 New York
 Rose, S. 1981 Montana
 Ross, E. S. 1983 California
 Ross, M. H. 1981 Virginia
 Roth, L. M. 1944 Massachusetts
 Rozen, J. G., Jr. 1956 New York
 Ruiter, D. 1976 Colorado
 Rush, P. A. 1984 Minnesota
 Russell, L. M. 1930 Maryland
 Rust, M. K. 1984 California
 Sabrosky, C. W. 1946 District of Columbia
 Sailer, R. I. 1943 Florida
 Sakimura, K. 1982 Hawaii
 Sands, D. P. A. 1984 AUSTRALIA
 Santana, F. J. 1966 District of Columbia
 Saugstad, E. S. 1979 Maryland
 Scanlon, J. E. 1952 Texas
 Scarbrough, A. G. 1971 Maryland
 Schaefer, C. W. 1985 Connecticut
 Schaffner, J. C. 1984 Texas
 Scharf, W. C. 1981 Michigan

- Schauff, M. E. 1980 District of Columbia
 Schmidt, C. H. 1969 North Dakota
 Schroder, R. F. W. 1976 Maryland
 Schwan, T. G. 1980 Connecticut
 Schwartz, M. D. 1985 New York
 Scudder, G. G. E. 1984 CANADA
 Sedman, Y. S. 1951 Illinois
 Segarra, A. E. 1985 Puerto Rico
 Selander, R. B. 1954 Illinois
 Shaffer, J. C. 1974 Virginia
 Shands, W. A. 1940 South Carolina
 Shanks, S. S. 1977 California
 Shaw, S. R. 1979 Massachusetts
 Shelly, T. E. 1982 California
 Shepard, H. H. 1927 Virginia
 Shewell, G. E. 1949 CANADA
 Shinohara, A. 1981 JAPAN
 Shockley, C. W. 1955 California
 Sholes, O. D. V. 1979 Massachusetts
 Skaptason, J. L. 1979 Virginia
 Slater, J. A. 1949 Connecticut
 Sleeper, E. L. 1976 California
 Sloan, M. J. 1983 District of Columbia
 Sluss, T. P. 1970 Colorado
 Smiley, R. L. 1964 Maryland
 Smith, C. F. 1967 North Carolina
 Smith, C. L. 1977 Georgia
 Smith, D. R. 1965* District of Columbia
 Snelling, R. R. 1968 California
 Sofield, R. K. 1983 Tennessee
 Solis, M. A. 1985 Maryland
 Sollers-Riedel, H. 1938* District of Columbia
 Southern, P. S. 1977 North Carolina
 Spangler, P. J. 1958* District of Columbia
 Spencer, C. B., Jr. 1955 Virginia
 Spicer, G. 1978 Illinois
Spilman, R. E. W. 1950 (1977) District of Columbia
 Spilman, T. J. 1950 District of Columbia
 Spinelli, G. R. 1983 ARGENTINA
 Staines, C. L., Jr. 1975 Maryland
 Stannard, L. J. 1948 Illinois
 Steffan, W. A. 1970 Idaho
 Stegmaier, C. E., Jr. 1965 Florida
 Steiner, W. E., Jr. 1979 Maryland
 Steinhauer, A. L. 1958 Maryland
 Steinly, B. A. 1983 Illinois
 Stewart, K. W. 1981 Texas
 Stewart, R. D. 1985 Maryland
 Steyskal, G. C. 1947 District of Columbia
 Stibick, J. N. L. 1966 Maryland
 Stimmel, J. F. 1979 Pennsylvania
 Stoetzel, M. B. 1971 Maryland
 Stone, A. 1931* Maryland
 Stonedahl, G. M. 1982 New York
 Stribling, J. B. 1983 Ohio
 Sturtevant, M. A. 1985 Illinois
 Surdick, R. F. 1979 Virginia
 Sutherland, C. M. 1974 New Mexico
 Sutherland, D. W. S. 1973 Maryland
Swartzwelder, E. B. 1948 (1974) Louisiana
 Sweeney, K. J. 1985 Maryland
 Taft, S. J. 1979 Wisconsin
 Teale, S. A. 1983 New York
 Tennesen, K. J. 1982 Alabama
 Thomas, D. B., Jr. 1983 Texas
 Thompson, F. C. 1968 District of Columbia
Thompson, J. V. 1953 (1985) New Jersey
 Thoms, E. M. 1985 Virginia
 Thornburg, M. C. 1961 Maryland
 Thorpe, K. W. 1980 California
 Tibbetts, T. 1955 Utah
 Tidwell, M. A. 1981 South Carolina
 Togashi, I. 1983 JAPAN
 Townes, G. F. 1956 South Carolina
 Townes, H. K. 1941 Florida
 Townsend, L. H., Jr. 1977 Kentucky
 Traub, R. 1947 Maryland
 Triplehorn, B. W. 1985 Virginia
 Triplehorn, C. A. 1972 Ohio
 Trumble, J. T. 1979 California
 Turner, C. E. 1985 California
 Turner, W. J. 1982 Washington
 Tyson, W. H. 1970 California
 Ulrich, H. 1978* WEST GERMANY
 Unzicker, J. D. 1983 Illinois
 Utmar, J. A. 1974* Maryland
 Valentine, J. F. 1983 Alabama
 Valley, K. 1976 Pennsylvania
 Vazquez, A. 1957 Virginia
 Venables, B. A. B. 1983 Maryland
 Venables, L. 1983 Maryland
 Villegas, B. 1977 California
 Vincent, D. L. 1980 Maryland
 Viraktamath, C. A. 1981 INDIA
 Voegtlin, D. 1981 Illinois
 Vogt, G. B. 1947 Mississippi
 Wagner, M. R. 1986 Arizona
 Waldbauer, G. P. 1983 Illinois
 Walker, H. G. 1941 California
 Wallenmaier, T. E. 1979 Maryland
 Waller, D. 1984 Louisiana
 Wallis, R. C. 1948 Connecticut
 Walton, M. 1937 Maryland
 Ward, R. A. 1975 District of Columbia
 Webb, D. W. 1981 Illinois
 Webb, R. E. 1967 Maryland
Weber, N. A. 1941 (1981) Florida
 Weems, H. V., Jr. 1953 Florida
 Weisman, D. M. 1956 District of Columbia
 Wendleton, D. S. 1965 Pennsylvania
 Wenzel, R. L. 1984 Illinois
 Werner, F. 1948 Arizona
 Werren, J. H. 1985 Maryland

- Wharton, B. 1981 Texas
Wheeler, A. G., Jr. 1974 Pennsylvania
Wheeler, G. C. 1949 Florida
Whitcomb, R. F. 1966 Maryland
White, G. B. 1977 Maryland
White, R. E. 1966 District of Columbia
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SEASONAL VARIATION OF BLACK PIGMENTATION UNDER THE
WINGS IN A TRUE BUG (HEMIPTERA: PENTATOMIDAE): A
LABORATORY AND FIELD STUDY¹

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Abstract. — In adults of the predaceous hemipteran, *Podisus maculiventris* (Pentatomidae), the abdominal terga vary from having no black pigment to being entirely black. Examination of wild *P. maculiventris* adults collected in pheromone-baited traps showed that black pigmentation of the tergum is most extensive in adults collected in fall and spring, and minimal in adults collected in mid-summer. Topical treatment of 1-day-old fifth-stage *P. maculiventris* larvae with juvenile hormone inhibited tergal blackening following ecdysis to the adult stage, suggesting that the black pigment is a true melanin. Under laboratory conditions, higher rearing temperatures inhibited melanization but photoperiod had little or no effect on the melanization of *P. maculiventris* adults. At any particular rearing temperature or field-collection date, the terga of females were significantly darker than the terga of males, but the melanization of males varied more than that of females over a range of rearing temperatures or collection dates. Body size was at most only weakly correlated with the degree of melanization in wild and laboratory-reared *P. maculiventris* males and females. The adaptive significance of melanism in *P. maculiventris* is discussed.

Variation in the cuticular melanization of insects is widespread (Kalmus, 1941a). Familiar examples include hyper-melanization of certain moths near smoke-polluted industrial centers (Kettlewell, 1961), geographical variation in the black elytral spots of ladybird beetles (Brakefield, 1984), and annual variability in the black bands of woollybear caterpillars thought by some to predict the severity of the coming winter (Borror et al., 1981). In this paper I will describe the melanism of adult spined soldier bugs, *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae), and examine possible causes of melanic variation in this true bug.

The most thorough study of color variation in an hemipteran insect was conducted by Knight (1923, 1924) on the twospotted stink bug, *Perillus bioculatus* (F.) (Pentatomidae). In *P. bioculatus* adults black and brown pigments are located in the cuticle and do not appreciably change after the initial hardening of the cuticle. The white, yellow and red colors are located in the epidermis and show through where the cuticle is transparent. The proportion of melanized and trans-

¹ Mention of a commercial product does not constitute an endorsement by the U.S. Department of Agriculture.

parent cuticle in *P. bioculatus* adults is regulated by temperature and only slightly affected by humidity; cooler rearing temperatures increase the area of melanized cuticle (Knight, 1924). Similarly, Novak (1955) found that the melanized sternal spots of adult milkweed bugs, *Oncopeltus fasciatus* (Dallas) (Hemiptera: Lygaeidae), are larger when the bugs are reared at lower temperatures, and that at the same rearing temperature the extent of melanization is greater in females than males. Knight (1923) reported that field collections of *P. bioculatus* corroborated his laboratory findings on the effect of temperature on melanization, and Dupuis (1949) noticed that larvae of several pentatomids are melanic when collected late in the season, but these observations were based upon relatively few field-collected specimens. Couturier (1938) reported that the black pigmentation of laboratory-reared fifth-stage *P. maculiventris* larvae was extremely variable, but he noticed no obvious differences in the pigmentation of adults. The availability of an artificial pheromone for the spined soldier bug (Aldrich et al., 1984) made possible a detailed examination of the seasonal melanic variation of wild *P. maculiventris* males and females. The ability to easily rear large numbers of this insect (Aldrich et al., 1978) enabled me to study the environmental and hormonal causes of *P. maculiventris* melanism in the laboratory.

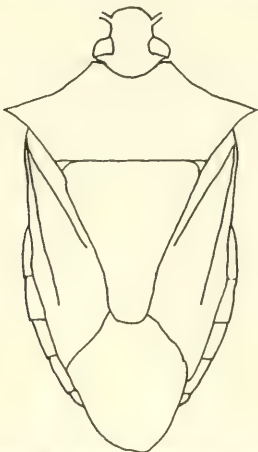
METHODS AND MATERIALS

Podisus maculiventris adults were caught in pheromone-baited traps near the Insect Physiology Laboratory, Beltsville Agricultural Research Center, from May, 1982, through April, 1985. Traps were deployed and pheromone prepared as previously described (Aldrich et al., 1984). Captured spined soldier bugs were stored in 70% ethanol or pinned for later scoring of melanization (Fig. 1). In 1982 and 1983, the width of the third abdominal tergite (excluding the connexiva) of melanically scored field-collected *P. maculiventris* adults was measured under a dissecting microscope to 0.1 mm using a mini-scale® (BioQuip Products, Santa Monica, CA). In April of 1984 and 1985, the melanically scored field-collected *P. maculiventris* adults were weighed to an accuracy of 0.1 mg. Daily temperature data were obtained from the United States weather station at the research center, approximately 3 kilometers from the study site.

Laboratory investigations were conducted on bugs from a stock colony started with individuals collected at the research center in 1982. The stock colony was maintained on *Tenebrio molitor* L. pupae (Coleoptera: Tenebrionidae) (Rainbow Mealworms, Compton, CA) at $26.7 \pm 1.5^\circ\text{C}$, 65% relative humidity (RH), and a 16:8 h light:dark (L:D) photoperiod. The critical period for commitment to melanization was determined by transferring fourth- and fifth-stage larvae of known age from the stock colony to an unlighted rearing chamber at 15.5°C and correlating adult melanism with the age of the larvae when transferred.

To test the effect of photoperiod on adult melanism, fourth instars were reared to the adult stage at reversed photoperiods but otherwise identical conditions. Two light-proof cabinets (46 × 31 × 107 cm) built one on top of the other inside a walk-in insectary ($29.4 \pm 2.8^\circ\text{C}$) were used for this experiment. Each cabinet was equipped with a fluorescent light (Sylvania F14T12-CW; 675 lumens); the top cabinet was cycled at 8:16 h L:D and the bottom cabinet was cycled at 16:8 h L:D. Hygrothermographs (Belfort Instrument Co., Baltimore, MD) were run simultaneously in each cabinet during the experiments.

DORSAL VIEW WITH WINGS



ABDOMINAL MELANIZATION UNDER WINGS

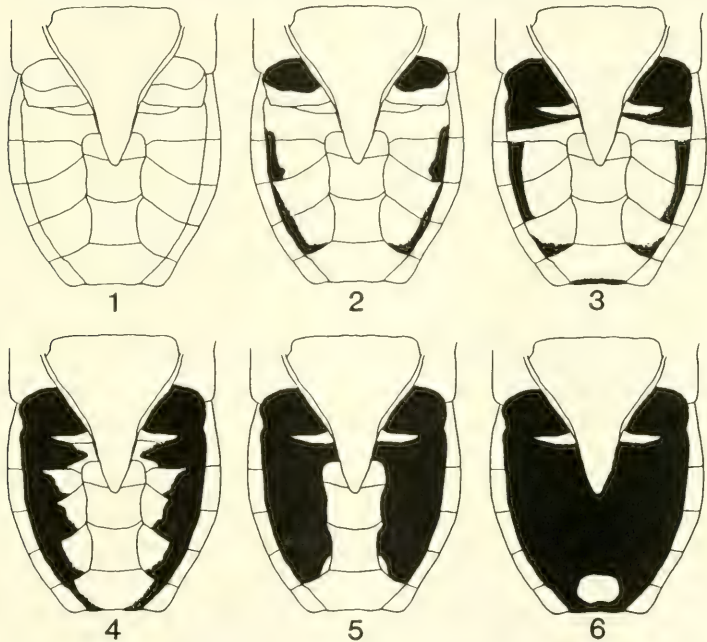


Fig. 1. Dorsal view of adult *Podisus maculiventris* with wings intact (top) and with wings removed (bottom). The abdominal melanization of adults was scored from unmelanized (score = 1) to almost entirely melanized (score = 6).

The effect of temperature on adult melanism was examined by rearing late fourth-stage larvae at 15.5, 21.1, 26.7 or 32.2°C. Larvae reared at 21.1, 26.7 and 32.2°C were housed in insectaries with 16:8 h L:D cycles, $65 \pm 5\%$ RH, and temperature fluctuations of $\leq 1.5^\circ\text{C}$. Larvae reared at 15.5°C were housed in an unlighted box at ambient RH with temperature fluctuations of $\leq 2.5^\circ\text{C}$. One set

of larvae was reared in the unlighted box at $35.8 \pm 4.7^\circ\text{C}$ to check for a photoperiodic effect on adult melanism.

Since melanization in some insects is inhibited by juvenile hormone (JH) (e.g. Truman et al., 1973), the effect of JH on the tergal melanization of *P. maculiventris* adults was tested. Female fifth-stage larvae (24 ± 8 h post-ecdysis) were removed from the stock colony, lightly anesthetized with CO_2 , and topically treated with 5, 0.5 or 0.05 μg JH-1 (methyl *cis*-10,11-epoxy-7-ethyl-3,11-dimethyl-*trans*, *trans*-2,6-tridecadienoate; Ayerst Laboratories, Montreal, Canada) in 1 μl of acetone. CO_2 -Anesthetized, acetone treated controls were run simultaneously with each set of treatments. Treated and control larvae were reared to the adult stage at 26.7°C , 16:8 h L:D and 65% RH. The area of melanized tergal cuticle of each adult was scored on the scale shown in Figure 1.

RESULTS

Field data.—From May, 1982, through April, 1985, a total of 4800 *P. maculiventris* adults were caught in or near pheromone-baited traps. Spined soldier bugs overwinter as adults and, at our study site, begin emerging in early April (Fig. 2, 1983). *Podisus maculiventris* larvae are occasionally caught in pheromone-baited traps (Aldrich, 1985), and third, fourth and fifth instars have been caught from mid-April to mid-May, demonstrating that overwintered adult females oviposit soon after emergence (Aldrich, unpubl. data). The first new generation of adults (F_1) appears from late May through June, followed by 1 or 2 more overlapping generations (Fig. 2, 1982 and 1983). About 10% of the adult bugs that emerge in the spring contain a larva of the tachinid fly parasitoid, *Hemyda aurata* Robineau-Desvoidy. Another tachinid, *Euclytia flava* (Townsend), parasitizes virtually all *P. maculiventris* adults caught in traps beginning about 2 weeks after the bugs emerge and, in fact, causes the bugs to avoid traps (Aldrich et al., 1984). Thus, the adults captured from late May through June must be predominantly newly ecdysed (F_1) adults because most of the overwintered adults probably do not survive beyond May.

From May, 1982, through April, 1985, a total of 1968 wild spined soldier bug adults were scored for tergal melanism and either measured or weighed. The abdominal terga of these adult spined soldier bugs varied from unmelanized to completely melanized (Fig. 1). Unmelanized tergal cuticle is translucent and appears brownish orange. As is characteristic of alate Hemiptera, the abdominal tergum of a *P. maculiventris* adult is covered by the wings except during flight (Fig. 1, top). There are thus no obvious differences in the coloration of adults having varying tergal melanization; dorsally the adults are dull yellow with small fuscous punctures and ventrally they are pale yellow with small reddish punctures (Blatchley, 1926).

Plotting the abdominal melanization score versus the collection date of male and female *P. maculiventris* adults reveals two important features of the population (Fig. 3). First, for adults collected at the same date, females are on the average more extensively melanized than males. Second, adults collected in the spring are more extensively melanized than those collected in the summer. The decline in tergal melanism with the advancing season, however, is not coincident with the appearance of the F_1 generation of adults. For example, in 1983 the transition in the melanization of field-collected bugs occurred from mid-June to

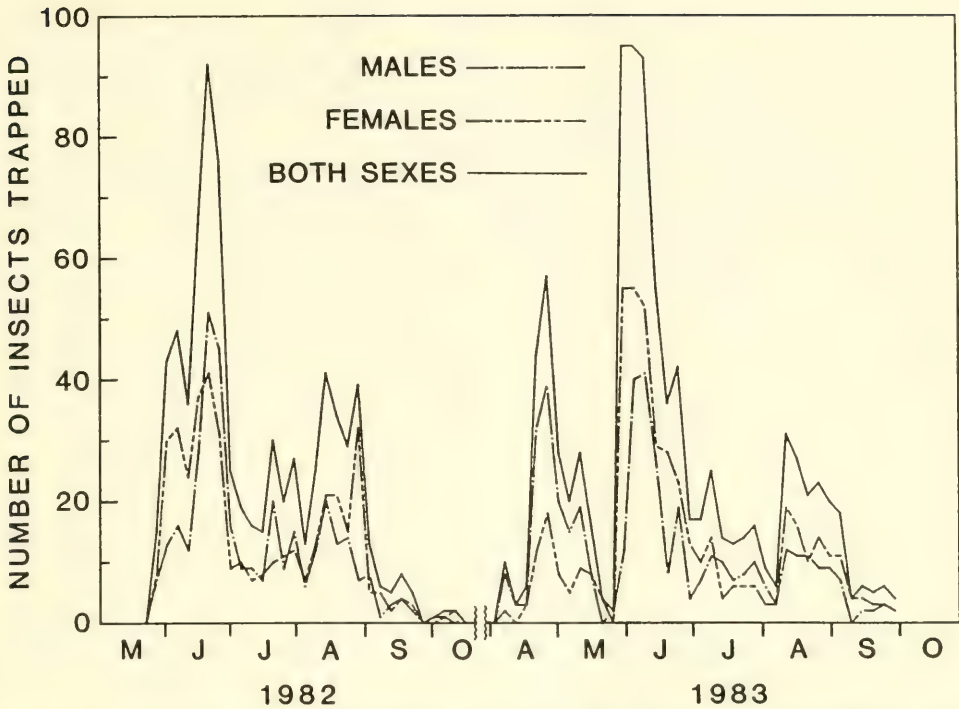


Fig. 2. *Podisus maculiventris* adults caught in or within 1 m of pheromone-baited traps monitored daily at the Agricultural Research Center, Beltsville, Maryland, during 1982 and 1983. Each point is a 5-day summation of the catches from seven sticky-wing traps.

mid-July (Fig. 3), but the peak collection of new adults occurred during late May and early June (Fig. 2). At the end of the trapping season the degree of tergal melanization and the confidence intervals for these points increased, but overwintered males and females were, on the average, more melanized than the adults caught the preceding September and October (Fig. 3).

The reduction in tergal melanism of *P. maculiventris* adults collected in May and June coincides with increasing daily temperatures during this period (Fig. 4). Prior to May 31, 1983, mean daily temperatures seldom exceeded 23.3°C (the transitional melanization temperature calculated from laboratory rearing data), whereas in June, July and August the daily mean temperature usually exceeded 23.3°C (Fig. 4). In September, mean daily temperatures were again below the transitional melanization temperature (Fig. 4), coinciding with the increase in the melanism of adults caught in September, 1983 (Fig. 3). The temperature curves for 1982 and 1984 exhibit patterns similar to that shown in Figure 4 for 1983, however, there were significant differences in the temperature extremes and the precise timing of temperature shifts from year to year. For example, during the period from August 15 through September 30 there were 40, 27 and 36 days when the mean daily temperature was 23.3°C or less in 1982, 1983 and 1984, respectively. Even though data for only 3 years are available, the correlation coefficient between the number of days $\leq 23.3^{\circ}\text{C}$ from August 15 through September 30 and the melanization score of males collected the following April was significant ($r =$

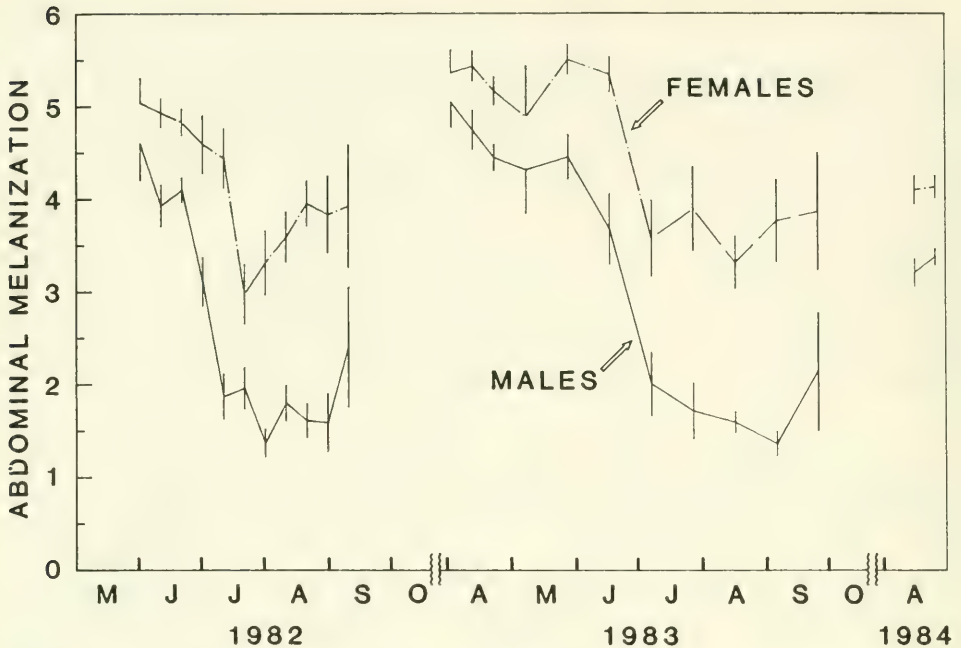


Fig. 3. A plot of melanization score versus collection date for *Podisus maculiventris* adults captured in or near pheromone-baited traps from May 1982 through April 1984.

0.9999, $P < 0.05$; melanization scores = 4.59, 3.32 and 4.18, respectively). For females this correlation was not significant ($r = 0.9516$; melanization scores = 5.27, 4.11 and 5.28, respectively).

Field-collected *P. maculiventris* females are significantly larger than males. For example, 95 females trapped April 17 through 19, 1984, weighed 47.4 ± 0.8 mg ($\bar{x} \pm \text{SEM}$), and 97 males trapped during the same period weighed 36.0 ± 0.6 mg ($t = 11.247$, $P < 0.001$). Based on the width of the third tergite, females were larger than males and there was a tendency for larger individuals to survive the winter; the width of females collected August 1 through September 24, 1982, was 4.75 ± 0.02 mm ($\bar{x} \pm \text{SEM}$, $n = 247$) versus 4.79 ± 0.02 mm ($n = 133$) for females collected April 3 through May 14, 1983, and the widths of males collected during the same periods, respectively, were 4.31 ± 0.02 mm ($n = 187$) and 4.33 ± 0.01 mm ($n = 227$). However, body size was never significantly correlated with the degree of melanization in field-collected bugs; e.g. $r = 0.0420$ ($n = 149$) for females and $r = 0.0064$ ($n = 268$) for males collected March 28 through April 21, 1985.

Laboratory data.—Transferring larvae of various ages from warm to cool rearing chambers indicated that the critical period for determination of adult melanism is approximately 24 h after ecdysis from the fourth to the fifth stage. Melanization of the abdominal tergum in *P. maculiventris* adults is first evident about 2 h after ecdysis. By 6 h post-ecdysis the final tergal melanization score can be discerned. After about 12 h, melanization of the tergum appears to be complete and does not visibly change for the rest of the life of the insect.

Rearing *P. maculiventris* larvae under reversed photoperiods had little or no

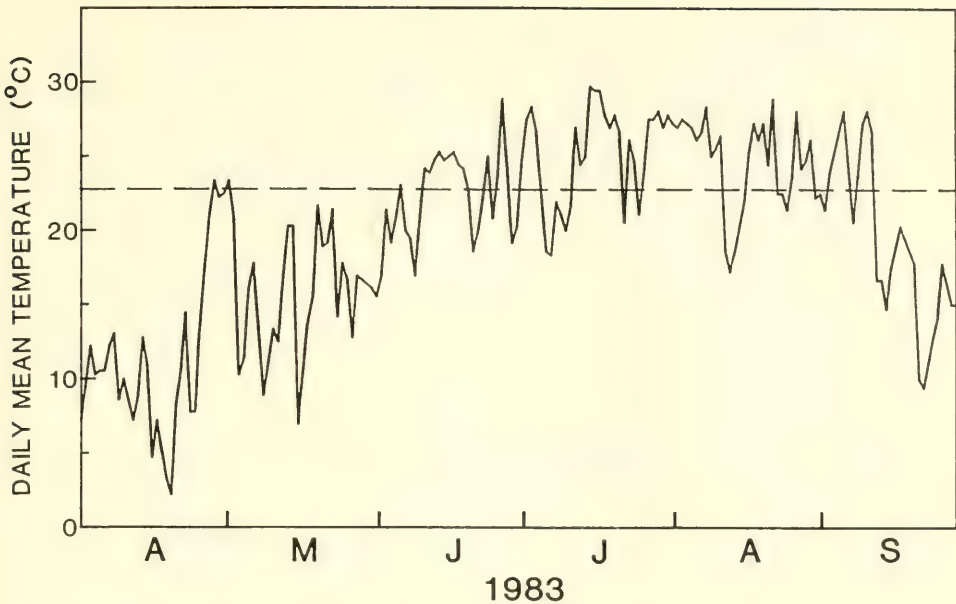


Fig. 4. Daily mean temperatures from April through September, 1983. The broken isothermal line is at 23.3°C, the transitional temperature for melanization in *Podisus maculiventris* adults.

effect on the melanism of adults (Fig. 5). For males reared at 16:8 h L:D ($n = 180$) there were about 5.5% more unmelanized individuals (score = 1) than for males reared at 8:16 h L:D ($n = 156$) (Fig. 5A). For females reared at 16:8 h L:D ($n = 179$) there were about 6.1% more individuals with melanization scores ≤ 3 than for females reared at 8:16 h L:D ($n = 172$) (Fig. 5B). The small excess of lighter adults under long-day conditions may be entirely due to the slight warming of the rearing cabinet caused by the longer light-on time. This experiment also demonstrated that at the same rearing temperature, in this case 29.4°C, the resulting tergal melanism of adult females ($\bar{x} \pm \text{SEM} = 3.45 \pm 0.09$, $n = 351$) is greater than that of males (1.18 ± 0.03 , $n = 336$).

The relationship of body weight to melanism for 576 *P. maculiventris* fourth-stage larvae reared to the adult stage at 26.7°C under long-day conditions is shown in Fig. 6. Over 85% of the males had a melanization score ≤ 3 at this rearing temperature and there is virtually no correlation between body weight and melanism (Fig. 6B). To the contrary, fewer than 8% of the females had a melanization score ≤ 3 and there is a significant positive correlation between body weight and melanism ($P < 0.01$) (Fig. 6A). Regression of body weight on melanism score reveals that body weight accounts for at most 8% ($r^2 = 0.0791$) of the natural melanic variation. As with field-collected bugs, laboratory-reared female bugs are larger than males (77.2 ± 1.0 mg and 52.9 ± 0.6 mg, respectively), but these laboratory-reared adults were much larger than overwintered field-collected *P. maculiventris* individuals.

The temperature at which late-stage *P. maculiventris* larvae are reared has a pronounced effect on the tergal melanism expressed in the adult stage (Fig. 7). At a given rearing temperature females are, on the average, more melanized than

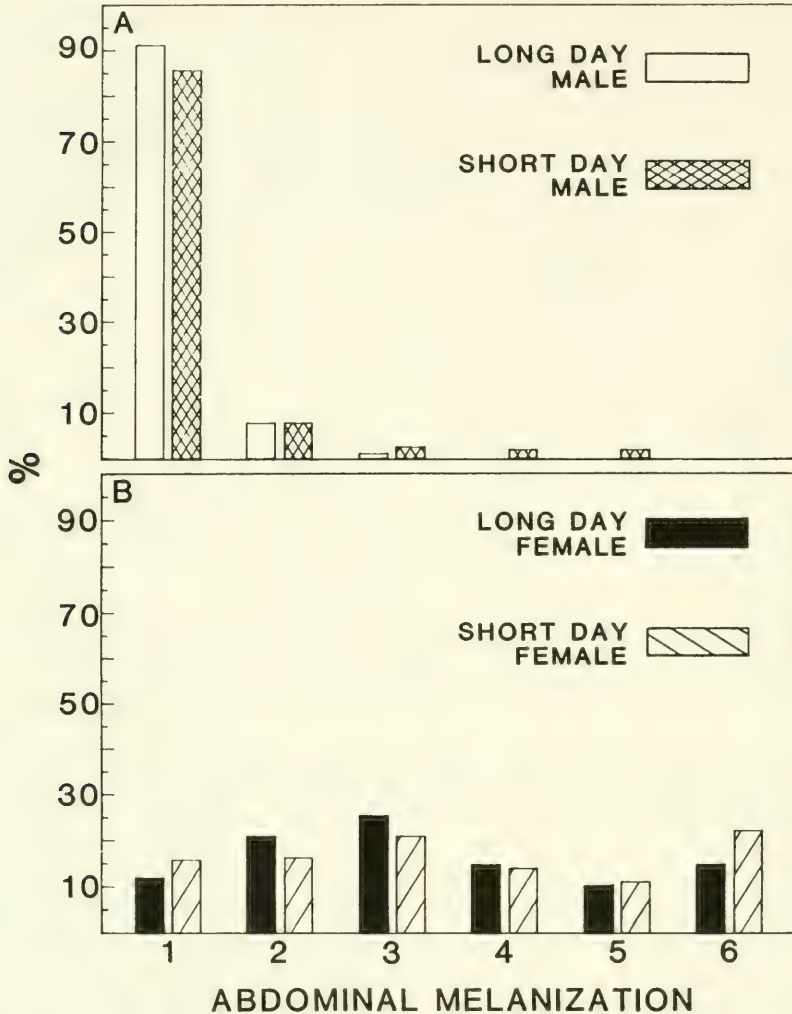


Fig. 5. Histogram of abdominal melanization for *Podisus maculiventris* adults reared at 29.4°C under either a long-day (16:8 h L:D) or a short-day (8:16 h L:D) photoperiod; A, males, B, females.

males. However, at different rearing temperatures the range of female melanization scores was relatively narrow, from 5.69 ± 0.17 at 15.5°C to 3.76 ± 0.15 at 32.2°C. On the other hand, the range of tergal melanism in males was much greater, from 4.82 ± 0.16 at 15.5°C to 1.21 ± 0.07 at 32.2°C. Although males are much more melanically variable than females, the average of the melanism range for each sex as plotted in Fig. 7 (i.e. score = 3 for males; score = 5 for females) falls at almost exactly the same temperature, 23.3°C. Therefore, 23.3°C has been considered the transitional melanization temperature for both sexes of *P. maculiventris* (Fig. 4).

Rearing fourth-stage larvae to the adult stage at 35.8°C in continual darkness produced unmelanized males (1.10 ± 0.08 , $n = 29$) and lightly melanized females (2.17 ± 0.24 , $n = 24$), verifying that temperature and not photoperiod is the primary determinant of adult melanism.

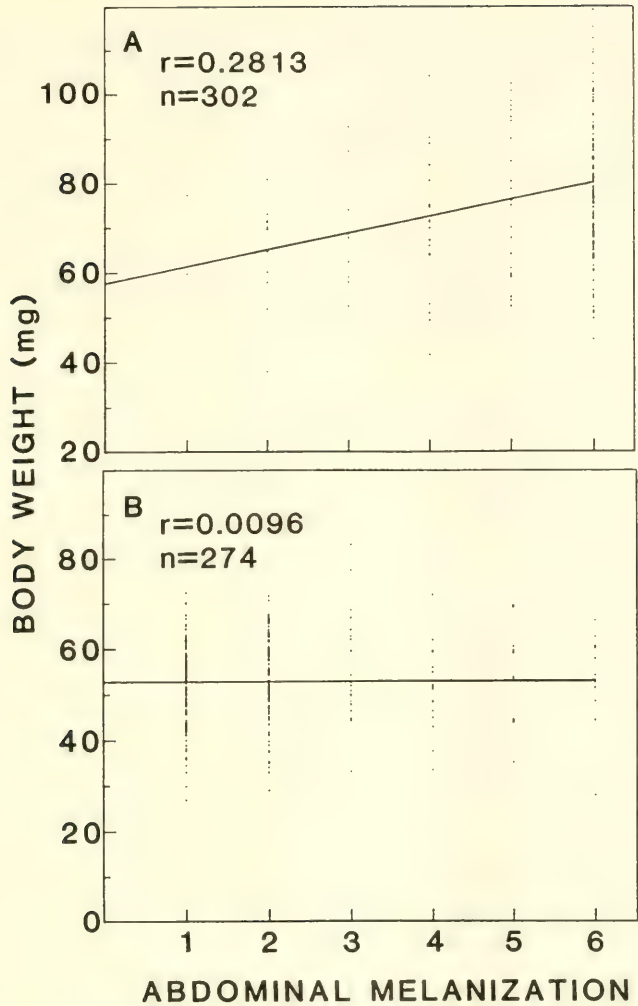


Fig. 6. Scatter plots of body weight versus melanization score for female (A) and male (B) *Podisus maculiventris* adults laboratory reared at 26.7°C and a 16:8 h L:D photoperiod (each point corresponds to one insect). Note the higher weight scale for females than for males.

Topical treatment of 24-h-old female fifth-instar *P. maculiventris* larvae with JH-1 inhibited melanization in the adult stage (Table 1). At a dose of 5 μg JH-1, most larvae failed to successfully molt and some that did exhibited juvenile characters. None of the 6 individuals which succeeded in molting normally after treatment with 5 μg JH-1 had any melanization of the abdominal tergum. At the 0.5- μg dose, adult tergal melanization was inhibited by 37% relative to controls. Furthermore, at this intermediate JH dose most individuals showing some degree of melanization had patches of unmelanized cuticle in otherwise melanized cuticular areas, creating a mottled appearance. Treatment with 0.05 μg JH-1 also significantly inhibited the area of the tergum melanized, but mottling of the melanic areas was infrequent. Although tergal pigmentation was inhibited by JH,

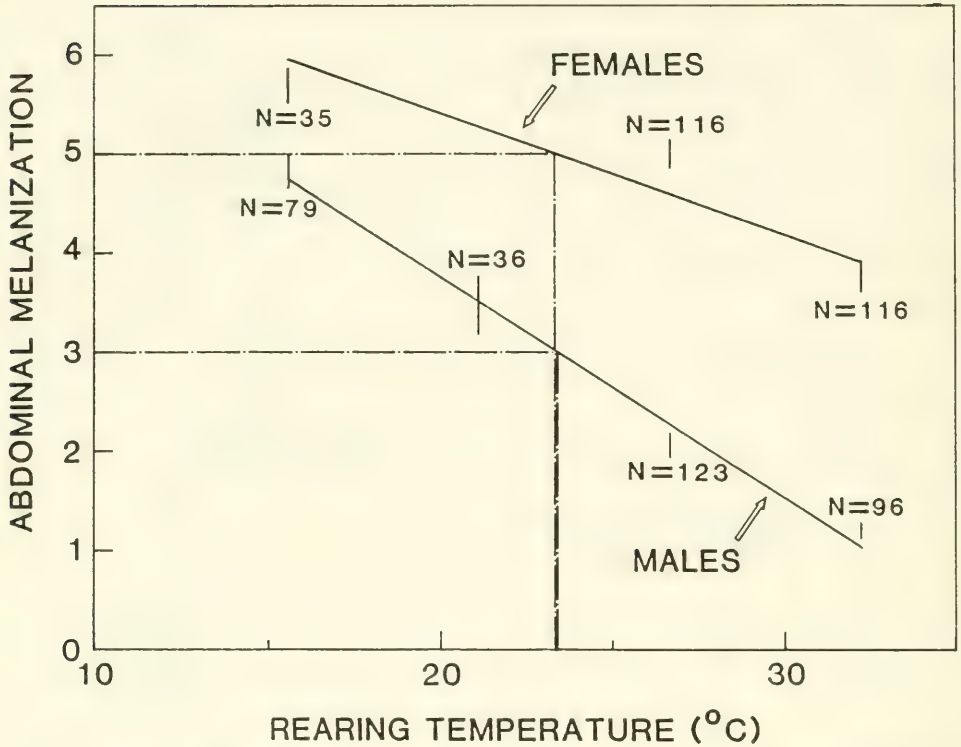


Fig. 7. The effect of rearing temperature on the abdominal melanization of adult male and female *Podisus maculiventris* under long-day conditions. Bars through points are standard errors of the means.

normal sclerotization of the cuticle was apparently unaffected; adults treated as larvae were mobile, fed normally and were long-lived.

DISCUSSION

Not all black pigments in insects are melanins (Kayser, 1985). Sclerotization can produce black cuticles in insects (Andersen, 1985), and melanization and sclerotization of cuticles are two independent processes in insects (Kayser, 1985). Rigorous proof of the existence of true melanins has been provided for only a few species and the black tergal pigment described here in *P. maculiventris* has yet to be chemically characterized. However, the inhibition of tergal pigmentation in adult spined soldier bugs by JH, with a critical period long before the onset of pigmentation, is similar to the pigmentation process in larvae of black mutant *Manduca sexta* (L.) (Lepidoptera: Sphingidae) (Truman et al., 1973), an insect shown to be truly melanic (Hori et al., 1984). The mottled appearance of the tergum in JH-treated *P. maculiventris* adults suggests that the black pigment is formed in discrete granules, another feature of melanization in black mutant *M. sexta* larvae (Curtis et al., 1984) and many truly melanic insects (Kayser, 1985). Furthermore, JH treatment did not inhibit sclerotization in *P. maculiventris* adults. Melanins in insect cuticle have only been found in the exocuticular part that is shed at ecdysis (Kayser, 1985). When adult milkweed bugs were artificially induced to molt by injection of an ecdysteroid, the exuviae contained the black spots

Table 1. Tergal melanism of female *P. maculiventris* adults treated topically with juvenile hormone as fifth-stage larvae (24 ± 8 h post-ecdysis) and reared under long-day conditions at 26.7°C.

Treatment	N	Melanization Score ($\bar{x} \pm \text{SEM}$)
CO ₂ control	93	4.39 $\pm$ 0.16
5 μg JH-1 ^a	13	1.00 $\pm$ 0.00
0.5 μg JH-1	29	2.79 $\pm$ 0.38 ^b
0.05 μg JH-1	73	3.68 $\pm$ 0.21 ^c

^a One nymph-adult intermediate obtained and 7 died prior to or during ecdysis.
^b Fourteen of 15 individuals scored ≥ 2 had unmelanized patches within areas of melanized cuticle.
^c Three of 62 individuals scored ≥ 2 had unmelanized patches within areas of melanized cuticle.

(Aldrich et al., 1981), implicating melanin as the black pigment in this hemipteran. Thus, the black tergal pigment in *P. maculiventris* adults is provisionally referred to as melanin.

The data demonstrate that melanism in *P. maculiventris* adults depends on the temperature experienced by early fifth-stage larvae, with cooler temperatures resulting in more melanic adults. Females are, on the average, more melanized but less melanically variable than are males. Photoperiod has little or no effect on melanization of spined soldier bug adults. In the field, individuals maturing during the warm summer days are less melanized than individuals maturing in the spring and fall. A similar correlation between seasonal temperatures and darkening has been reported for adult *Lygus* bugs (Hemiptera: Miridae), but in these insects the darkening, although irreversible, spreads continuously in the tissue underneath the transparent cuticle with age (Wilborn and Ellington, 1984). Sampling of *P. maculiventris* revealed that adults caught in April were much more melanized than those caught the previous September and October. Since sampling required attraction of adults to a synthetic pheromone, it is probable that late-maturing adults (likely to be melanic) were committed to diapause and unresponsive to pheromone. If this is the case, sampling late in the season is biased toward less melanized individuals.

The reasons for melanic variation in *P. maculiventris* are obscure. In the two-spot ladybird beetle (Brakefield and Willmer, 1985) and other insects (Casey, 1981) geographical and seasonal variation in melanism is involved in regulation of body temperature. Melanin may also serve to shield insects from harmful ultraviolet radiation (Kayser, 1985), and the increased melanization of insects near smoke-polluted cities enhances crypsis (Kettlewell, 1961). Each of these functions seems inapplicable as a rationale for the melanism of spined soldier bugs because the tergum is always covered by the wings when the insects are not flying and the wing cuticle that is exposed renders the bugs cryptic in their forest habitat. Moreover, when laboratory-reared *P. maculiventris* adults held at 15.5°C were set free on a sunny day, they did not open their wings to bask in the sun (unpubl. observation). Although spined soldier bugs are capable of flying at least several hundred meters nonstop (Aldrich et al., 1984 and unpubl. observation), usually the bugs make repeated short flights, a circumstance under which it is doubtful that tergal melanization appreciably affects thermoregulation. Cott (1940) considered the brightly colored terga of certain Hemiptera (e.g. Coreidae, Nepidae) to be adaptive as “flash colors” to startle predators. Even granting that startling

predators confers a selective advantage upon spined soldier bugs possessing an orange tergum (which seems dubious), there must be some counter selection favoring melanism.

Although melanic variation is much greater for *P. maculiventris* males than females, Evans (1982) found that the body size of spined soldier bug females is much more variable than that of males. This suggests that melanic variation in *P. maculiventris* may involve phenomena affected adversely by increasing the ratio of body surface area to mass, such as thermoregulation or desiccation. But, as argued earlier, a thermoregulatory role for melanism in *P. maculiventris* adults seems unlikely. There is some evidence that melanized cuticle in insects is more resistant to desiccation (Kalmus, 1941a, b), a hypothesis now being tested for *P. maculiventris* adults.

ACKNOWLEDGMENTS

I thank Dr. M. S. Blum, Department of Entomology, University of Georgia, for kindling my interest in hemipteran color variation. I am also grateful to Joseph Sexton and Susan Wilzer for long, tedious hours of technical assistance.

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A NEW *STRONGYLUM* KIRBY FROM THE PUERTO RICAN BANK
(COLEOPTERA: TENEBRIONIDAE)

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Abstract.—*Strongylium paddai*, new species, is described from the northern Virgin Islands. A key to the species of *Strongylium* known from the eastern Antilles is provided. Biogeographic implications of this species for the evolution of Puerto Rican Bank wood-borers suggest that larval rafting may be of more importance than adult flight in maintaining inter-island contact.

While preparing a faunal treatment of the Tenebrionidae of the Virgin Islands, an undescribed species of *Strongylium* was discovered in material assembled from several sources. This species is especially interesting because of its biogeographic implications.

The genus *Strongylium* Kirby, with over 700 described species world-wide is the largest genus of Tenebrionidae (Gebien, 1948: 519). The Neotropics are especially rich in species, with over 320 described, but only nine are yet known from the West Indies. Of these, four are known only from Cuba (Blackwelder, 1945: 545). All of the Cuban species are various shades of blue or purple, and Mäklin (1864) gives comparative diagnoses for all four. Marcuzzi's (1962: 39) record of *Strongylium* cfr. *curticorne* Champion from Cuba probably belongs to one of these species.

The other five known West Indian species occur on the eastern Antilles, from Puerto Rico to Martinique. All are castaneous to black with metallic greenish-bronze reflections. Since only two were treated by Mäklin, a key to these species is presented.

KEY TO THE *STRONGYLUM* OF THE EASTERN ANTILLES

1. Eyes large, nearly contiguous above, elytra variable 2
- Eyes smaller, not nearly contiguous above; elytra uniformly colored ... 3
2. Elytra with two yellow maculae; scutellum finely punctate; 7–7.25 mm. Guadeloupe *S. delauneyi* Fleutiaux and Sallé
- Elytra uniformly colored; scutellum densely punctate; 21 mm. Martinique *S. chalcopterum* Mäklin
3. Base of elytra 1.5 times as wide as base of pronotum; pronotum as long as wide, with a pit on each side of disk; face strongly rugose between eyes; 5.25 mm. Guadeloupe *S. guadeloupense* Gebien
- Base of elytra only a little wider than base of pronotum; pronotum dis-

- tinctly wider than long, disk without pits; face between eyes simply punctate 4
4. Elytra with striae reduced or obsolete at apical $\frac{1}{4}$ (Fig. 2); face finely to moderately punctate, punctures often separated by more than 2 diameters; 8–10 mm. Puerto Rico *S. pulvinatum* Mäklin
- Elytra with striae deep to apex (Fig. 1); face coarsely punctate, punctures separated by about 1 diameter; 8–12 mm. Northern Virgin Islands *S. paddai* n. sp.

***Strongylium paddai* Ivie and Triplehorn, NEW SPECIES**

Fig. 1

Description.—Holotype male: Elongate, robust, piceous with greenish-bronze metallic reflections, shining. Head moderately coarsely punctate, except for a narrow, irregular, impunctate line on frons, punctures becoming distinctly strigulose on vertex; eyes large, laterally prominent, strongly reniform, separated dorsally by a distance subequal to length of 4th antennomere; genae slightly reflexed above antennal insertions; clypeus truncate apically, hind margin closely approaching eyes (about 2 facets distance); antenna reddish-brown, long, slender, ratio of antennomeres from base to apex: 2:1.5:6:4:4:4:4:4:4:5. Pronotum transverse ($\frac{2}{3}$ broader than long), lateral margins feebly sinuate, without trace of marginal bead, broadest anterior to middle, anterior margins broadly, shallowly emarginate, thickened medially, anterior angles rounded, basal margin feebly emarginate, thickened and subtended by a deep groove; basal angle nearly right, surface coarsely and densely punctured, most punctures separated by less than their diameters, continuing on hypomeron without obvious change in size and density; prosternum almost smooth, process transversely, deeply concave between coxae. Elytra with striae deeply sulcate on disc, punctures deep with diameters subequal to $\frac{1}{5}$ width of intervals; decreasing gradually in size apically in correspondingly shallower sulci; intervals moderately convex basally, feebly so apically, epipleural fold obsolete at extreme base, continuous to apex. Metasternum and abdominal sterna finely, shallowly, sparsely punctate. Legs moderate, stout, coarsely punctate. Length: 8.8 mm, width: 3.3 mm.

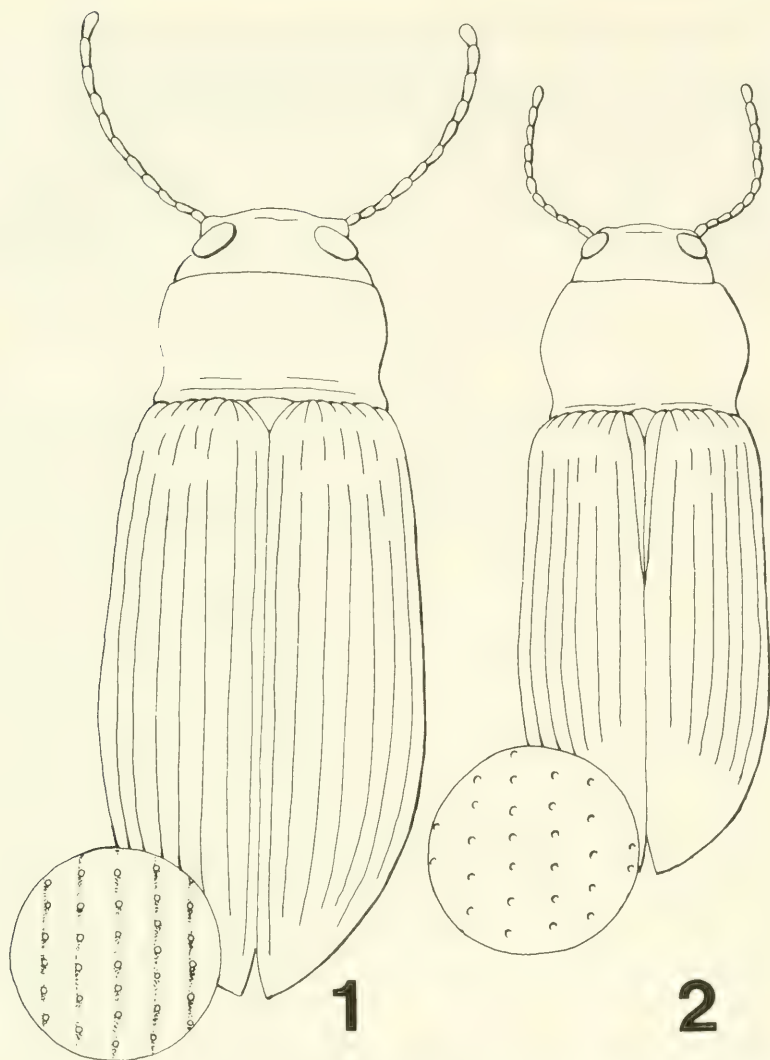
Allotype, female: Similar to male but with smaller, less prominent eyes; distance separating eyes dorsally subequal to combined length of antennomere 2 and 3; and the apical antennomere shorter than in male. Length: 8.8 mm, width: 3.2 mm.

Variation.—Background color varies from ferruginous to piceous, and the metallic reflections, which are most noticeable on the head, are sometimes absent. Size, length 8–12 mm, width 2.7–4.4 mm, appearing to be independent of sex.

Diagnosis.—The unicolorous, ferruginous to piceous integument with greenish-bronze metallic reflections, complete elytral striae, transverse pronotum and simply punctate face will distinguish this species from all previously described West Indian *Strongylium*.

Etymology.—This species is named in honor of Darshan S. Padda, Director of the Virgin Islands Experiment Station and Virgin Islands Cooperative Extension Service, St. Croix, who first suggested a faunal investigation of Virgin Island insects to one of us (MAI).

Holotype [♂].—Virgin Is., St. John; Lameshur Bay, VIERS; 08 March 1984;



Figs. 1-2. 1, *Strongylium paddai* Ivie and Triplehorn. 2, *Strongylium pulvinatum* Mäklin. Insets show details of striae on apical third of elytra.

blacklight trap; W. B. Muchmore colr. Allotype [♀]: Virgin Is., St. John; Lameshur Bay, VIERS; 15 August 1980; at uv light, M. A. Ivie. Deposited in NMNH.

Paratypes (33).—Virgin Islands: ST. JOHN: 15, Lameshur Bay, Virgin Islands Ecological Research Station, various dates III-1984, W. B. Muchmore; 2, *ibid.* 18-27 VII-1972, A. B. Gray; 1, Est. Carolina, NW of Coral Bay, 250 ft., 16 V, 1982; 1, Cinnamon Bay, 9-15 IV 1979, S. Foster and N. Hinnebusch; 2, Francis Bay, 25 III 1958, J. F. G. Clark; 1, Lind Point, 26 II 1962, H. B. Muller; 1, Virgin Island Nat'l Park, 28 I 1970; 1, near Trunk Bay, 15 VIII 1962; 1, no exact location, 18 VI 1971. ST. THOMAS: 2, Red Hook, 27 VII and 16 VIII 1979, M. A. Ivie; 1, Charlotte Amalie, 9 VI 1979, M. A. Ivie; 2, Frenchmans Bay Est., 750 ft., VI

1979, M. A. Ivie. PETER ISLAND (BRITISH VIRGIN ISLANDS): 1, Little Bay, 30 III 1958, J. F. G. Clark. ANEGADA: 1, Flamingo Pond, 23 VIII 1980, M. A. Ivie. TOBAGO ISLAND (U.S. VIRGIN ISLANDS): 1, 2 IV 1966.

Paratypes are deposited in BMNH, MAIC, MCZC, NMNH, OSUC, and VIER.

Biology.—A single *Strongylium* larva, presumed to be *S. paddai*, was extracted by Berlese funnel from material sifted from a very dry, crumbly rotten stump near the beach at Red Hook, 27 VII 1980, St. Thomas (specimen in MAIC). An adult *S. paddai* was found beneath the intact bark of the same stump.

Adults have also been taken at both white and ultraviolet light, and in Malaise traps.

Discussion.—*Strongylium paddai* belongs to Mäklin's Div. V A ** (hereafter referred to as the *pulvinatum* species-group), whose only previously included species is *S. pulvinatum* (for a diagnosis, see Mäklin, 1864). A species-group of such a widespread genus apparently endemic to the Puerto Rican Bank is surprising, given the rather small representation of the genus in the West Indies. The phylogenetic distance implied by the other West Indian species being placed in other Divisios (Mäklin's category roughly corresponding to a subgenus), and the isolated geographic distribution of the *pulvinatum* species-group, implies a zoo-geographic history independent of other species of West Indian *Strongylium*. Hypotheses of origin of the lineage, both phylogenetic and zoogeographic, must await further studies, but the intraspecies-group clade is of interest to studies of the Puerto Rican Bank fauna.

A post-Pleistocene eustatic rise separated Greater Puerto Rico into many smaller islands (Puerto Rico and the northern Virgin Islands) roughly 8–10,000 y.b.p., with the northern Virgin Islands remaining coalesced for ca. 2000 years (Heatwole and MacKenzie, 1967). In small, flightless, litter-dwelling beetles [e.g. *Nesopalla* (Ceratocanthidae) and *Antillomonomma* (Monommidae)], this is hypothesized to be sufficient isolation and time to explain endemic sister-species in Puerto Rico and the northern Virgin Islands. However, until now, no group of flighted wood-boring beetles has been found to have endemic sister-species on these two island groups. The relatively small distance involved (ca. 64 km), and ability of wood-boring Coleoptera larvae to survive inside floating wood (Heatwole and Levins, 1972; Ivie and Miller, 1984) seemed sufficient for the genetic contact needed to maintain specific identity.

The case of *Strongylium paddai* and *pulvinatum* is the first discovered to challenge this view. Although *Strongylium* are wood-borers, the larvae are associated with decaying wood (Triplehorn and Spilman, 1973). The larval *S. paddai* was found in very crumbly, rotten wood. This larva was small and probably had not been in the wood since it was sound. This habitat would waterlog and sink very quickly, not serving well as a rafting habitat. Since the capacity for flight in *S. paddai* is unchallengeable, it seems that the assumed genetic contact between other species of Puerto Rican Bank wood-borers is more likely to be the result of larval rafting than adult flight capacity, as supported by evidence reported by Heatwole and Levins (1972).

Material cited is deposited in the following museums, as indicated by the associated acronyms: National Museum of Natural History, Washington (NMNH); British Museum (Natural History), London (BMNH); Museum of Comparative

Zoology, Cambridge (MCZC); Virgin Islands Ecological Research Station, St. John (VIER); The Ohio State University, Columbus (OSUC); Michael A. Ivie, private collection, Bozeman (MAIC).

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**VIOLENT WAVE ACTION AND THE EXCLUSION OF
EPHYDRIDAE (DIPTERA) FROM MARINE TEMPERATE
INTERTIDAL AND FRESHWATER BEACH HABITATS**

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Abstract.—Evidence from a study of ephydriids in temperate habitats supports the hypothesis that insects are physically excluded from wave-disrupted marine and freshwater habitats (Buxton, 1926; Hinton, 1976a). Regularly flooded Scandinavian supralittoral (watt) and marine rock habitats and Lake Erie beaches exposed to violent wave action have the lowest shore-fly (Diptera: Ephydriidae) richness. Marine and freshwater richness values increase with shore elevation and distance from disrupted beach habitats. A comparison of Scandinavian and Nearctic shore-fly communities with the Sorenson index of similarity indicates the resident populations were distinctive species assemblages. Behavioral avoidance, habitat preferences, and shortened developmental cycles presumably reduce immature mortality and exposure to periodic violent inundation.

Historically, insect competition with the Crustacea, osmoregulation problems, and periodic inundation have been considered the major constraints limiting insect colonization of marine habitats. In 1926, Buxton proposed that the physical violence of wave action excluded insects from intertidal areas. Hinton (1976a) reasserted that violent wave action has restricted insect colonization in marine habitats. Additionally, Hinton (1976b) suggested that violent wave turbulence, extreme, and rapid depth variations associated with regular flooding and drying have limited colonization of exposed intertidal zones. Although Buxton (1926) and Hinton (1976a, b) supported the wave action hypothesis, they did not present quantitative evidence substantiating their suppositions.

Beach and intertidal zones are submerged by periodic tides and/or occasional storms. During submersion and emersion episodes, beach and intertidal organisms experience fluctuating physical, chemical, and biological conditions. These conditions vary between the upper and lower limits of the intertidal range and are related to the magnitude of tidal fluctuation, duration, and wave action. The supralittoral (Neumann, 1976) division of the intertidal zone is irregularly flooded during storms and the marine tidal extremes of the equinoxes. The supralittoral fringe of the midlittoral is submerged every two weeks by the high waters of spring tides. The midlittoral is inundated by tides once or twice daily, and its sublittoral fringe is exposed only by the low waters of spring tides. The land-to-sea dimensions of these intertidal divisions depend on the amplitude of local tides and shore topography (Neumann, 1976).

Intertidal and freshwater beach habitat substratum characteristics are related to the degree of wind exposure, wave action intensity, and climatic factors (Neumann, 1976). Turbulent wave action associated with tides and storms severely disrupts the substratum. Commonly encountered disruptive processes include vertical mixing, horizontal displacement, erosion, and abrasion of substratum components.

Tidal and storm wave intensity is reduced significantly in sheltered marine environments. Sheltered environments include leeward coastal areas, bays, estuaries, lagoons, mangrove swamps, and saltmarshes. Saltmarshes, primarily confined to temperate regions, are expanses of herbs and shrubs periodically inundated by tides (Foster and Treherne, 1976). Saltmarshes form in areas sufficiently sheltered to allow the deposition and accumulation of fine inorganic and organic particulate matter (Teal and Teal, 1969). Although inundated periodically, the saltmarsh substratum is not severely disrupted, and, consequently, a variety of salt-tolerant plant species colonize the habitat. Saltmarsh habitats and niches are relatively stable compared to those in exposed intertidal zones. The greater insect abundance in saltmarshes suggests that salinity is a minor factor preventing insect colonization of the exposed intertidal zone (Hinton, 1976a). Neumann (1976) reported that salinity was not the limiting factor controlling intertidal vertical distribution of chironomids.

Several hundred insect species have colonized marine habitats (Cheng, 1976; Hinton, 1976a, b). The predominant proportion of colonizing insect species in marine habitats have originated in terrestrial rather than aquatic habitats. Hinton (1976a) considered aquatic and terrestrial environments to have comparable moisture levels. Submersion of terrestrial environments for prolonged periods is not a rare or isolated event (Hinton, 1976a). Hinton (1960) reported the more common presence of respiratory plastrons among terrestrial than aquatic insects.

A large majority of marine paurometabolous insects are found only in sheltered habitats (Table 1). Most water-strider species (Hemiptera: Gerridae) have invaded coastal water-bodies that have transient contact with the sea. These habitats include saltmarsh ditches and pools, brackish ponds and lakes, coastal rock pools, and brackish lagoons (Anderson and Polhemus, 1976). Additionally, gerrid species are found in estuaries, mangrove swamps, and sheltered bays (Anderson and Polhemus, 1976). The near-shore distribution of water-striders has been related to the degree of disturbance, water currents, wave action and wind exposure (Anderson and Polhemus, 1976).

Polhemus (1976) listed 20 species of Saldidae occurring in quiescent marine habitats and 8 species in the intertidal zone. In addition to the sheltered habitats listed in Table 1, saldids have been infrequently collected in mangrove swamps and beach-dune habitats. Species found in the intertidal zone are restricted to coral and rock reefs (Polhemus, 1976). Commonly, intertidal saldid species take refuge in volcanic rock pockets and crevices which reduce the risk of being swept out to sea by tidal currents. Uhler (1884) reported the retreat of *Pentacora signoreti* (Guerin) (Hemiptera: Saldidae) before the oncoming tide. Also, eleven species of intertidal (coral rock coast) *Halovelia* (Hemiptera: Veliidae) take refuge from wave action in holes of submerged rocks containing small pockets of air (Kellen, 1959).

Among holometabolous insects, the Diptera are most frequently collected in marine environments. Mosquito (Culicidae) adults and larvae are encountered

Table 1. Distribution of Marine Hemiptera.†

Family	Number of Species in Exposed Intertidal Zone	Number of Species in Sheltered Habitats*
Gerridae	0	54
Mesoveliidae	2	1
Veliidae	12	6
Saldidae	8	20
Gelastocoridae	1	2
Omaniidae	3	0
Total =	26	83

† Data extracted from Cheng, 1976.

* Sheltered habitats include: saltmarshes, estuaries, mangrove swamps, brackish pools above high tide mark, and leeward beaches.

primarily in mangrove swamps, saltmarshes, and brackish intertidal pools above the high tide mark (O'Meara, 1976). Approximately 100 mosquito species (Culicidae) have been identified from such sheltered marine environments.

Along the Atlantic and Gulf coasts of the United States, the larvae of no-see-ums (Ceratopogonidae) have been found in the intertidal zones of sheltered beaches (Goulding et al., 1953; Jamnback et al., 1958; Jamnback and Wall, 1958; Wall and Doane, 1960; Linley and Adams, 1972). Of the 60 marine ceratopogonid species, no species are known to occur where sand is subject to heavy wave action (Linley, 1976). Additionally, simulated wave action caused *Culicoides melleus* pupae to burrow more deeply into the substratum (Linley and Adams, 1972a; Dyce and Murray, 1967).

The non-biting midges (Chironomidae) have exhibited the greatest success in colonizing the marine littoral and sublittoral zones. In general, chironomid larvae have been found in various moss-like or felt-like filiform algae that thickly encrust rock or coral-reef substrata (Neumann, 1976). This association apparently is independent of algal species (Neumann, 1976). Many benthic marine midges construct a protective case in the algae (e.g. *Pontomyia* spp.).

In the exposed intertidal zone, adult midge activity may be interrupted by wind and heavy surf. The severity of weather and wave action has been mitigated by several unusual adaptations (Neumann, 1976). Those adaptations, discussed by Neumann (1976) include: synchronization of emergence time with calm weather or with benthic habitat exposure; dislocation of the swarming site to protected locations; short adult life (a few hours), so emergence, mating, and oviposition coincide with the exposure of intertidal habitat; resistance to submersion by wave action; oviposition behavior and the characteristics of the egg mass.

Only five Coelopidae species have been reported from marine beaches (Dobson, 1976). The seaweed (or kelp) flies (Coelopidae) utilize marine algae washed ashore into wrack rows by intensive wave action. Throughout the year, these transient rows of decaying plant material are used for food and shelter (Backlund, 1945). These wrack rows are usually removed within two to four weeks by storms or periodic high tides. Within the sheltering wrack, kelp flies complete development within 12 days (Dobson, 1976). This shortened life cycle enables the kelp fly to utilize a transient food supply and avoid severe wave action.

Table 2. Ephydriidae (Diptera) found in aquatic habitats on Lake Erie shores.

Species	Sedge-Meadow		Marsh-Reed		Wave Zone Sand Beach		High Sand Beach		Limnic Wrack	
	Num- ber N	Rela- tive Abun- dance R.A.	Num- ber N	Rela- tive Abun- dance R.A.	Num- ber N	Rela- tive Abun- dance R.A.	Num- ber N	Rela- tive Abun- dance R.A.	Num- ber N	Rela- tive Abun- dance R.A.
<i>Allotrichoma simplex</i>	1	r					1	r		
<i>Dichaeta caudata</i>	1	r	2	r						
<i>Discocerina obscurella</i>	10	occ			4	r	3	occ	26	a
<i>Ephydra riparia</i>	27	a	1	r						
<i>Hecamedoides glaucellus</i>					35	c	58	va	30	a
<i>Hydrellia crassipes</i>			2	r						
<i>Hydrellia griseola</i>	8	occ							1	r
<i>Hydrellia ischiaca</i>			3	r						
<i>Hydrellia tibialis</i>	2	r								
<i>Hydrochasma buccatum</i>							1	r		
<i>Hydrochasma leucoproctum</i>					1	r	18	a	12	c
<i>Lytogaster excavata</i>			1	r						
<i>Notiphila erythrocer</i>			7	r						
<i>Notiphila loewi</i>							1	r		
<i>Notiphila macrochaeta</i>			1	r						
<i>Notiphila pallidipalpis</i>			1	r						
<i>Notiphila scalaris</i>			3	r						
<i>Notiphila sicca</i>			3	r						
<i>Notiphila vittata</i>	1	r								
<i>Ochthera mantis</i>	1	r	2	r						
<i>Paracoenia bisetosa</i>	2	r								
<i>Paracoenia fumosalis</i>	1	r								
<i>Paralimna punctipennis</i>			3	r						
<i>Parydra breviceps</i>	2	r	5	r						
<i>Parydra quadrituberculata</i>	14	occ	29	occ	2	r	1	r	2	r
<i>Philygria debilis</i>					3	r	3	occ		
<i>Polytrichophora orbitalis</i>	12	occ							4	occ
<i>Scatella favillacea</i>	78	va	176	va	95	va			1	r
<i>Scatella obsoleta</i>	9	occ	1	r	200	va	5	occ		
<i>Scatella paludum</i>	2	r	14	r	2	r				
<i>Scatella stagnalis</i>	9	occ	237	va	3	r	2	r	54	va
<i>Setacera atrovirens</i>			1	r						
Total	180		492		345		93		130	

Simpson (1976) listed 72 marine Nearctic shore-fly (Ephydriidae) species. Approximately equal numbers of ephydrid species exhibited a preference for the exposed intertidal and quiescent marine environments. Although 22 species have been collected in intertidal areas, little information has been accumulated characterizing larval habitat requirements in North America.

In this paper, I review literature that suggests violent wave action influences the colonization and distribution of many marine and freshwater insects. Evidence is presented that suggests violent wave action is an additional constraint limiting the colonization of the Ephydriidae (Diptera) in marine and freshwater lake habitats. The distribution of Scandinavian marine shore-fly communities are com-

Table 3. Species richness values (s) of ephydrid faunas in Scandinavian marine and Lake Erie aquatic habitats.

Marine Habitats	Species Richness (s)	Aquatic Habitats	Species Richness (s)
Watt (supralittoral)	5	Limnic wrack	8
Rock pool (supralittoral)	6	Wave zone-sand	9
Wrack	14	High sand beach	10
Marsh	13	Sedge-meadow	17
Grass pool	17	Marsh-reed	19
High sand beach	26		
Sand pool	20		
Hockenya	8		

pared with the Sorenson similarity index. Additionally, Nearctic ephydrid distribution, relative abundance, and similarity indices are described for quiescent and disturbed freshwater lake habitats.

METHODS AND MATERIALS

Shore fly adults were collected with a modified aerial sweep net (Regensburg, 1977) and immediately killed with ethyl acetate at the site. Sampling was concentrated at Mentor Marsh and Geneva State Park in Ohio, and Presque Isle Park, Pennsylvania. Mentor Marsh and Geneva State Park marsh-reed and sedge-meadow habitats were contiguous with Lake Erie. These habitats in Ohio and Pennsylvania were characterized by vegetation types and/or substrate constitution (Steinly, 1978). The sedge-meadow (Weaver and Clements, 1938; Deonier, 1965; Scheiring and Foote, 1973; Regensburg, 1976; Steinly, 1978) was dominated by *Carex* Linnaeus species, *Juncus effusus* Linnaeus (common rush), *Glyceria striata* (Lamarck) A. S. Hitchcock (Manna grass), and *Scirpus cyperinus* (Linnaeus) Kunth. The marsh-reed habitat had large quantities of decaying plant debris floating on the water or associated with a moist substrate. The dominant macrophyte was *Typha latifolia* Linnaeus (broad-leaved cattail). The Scandinavian marine (Dahl, 1959) and Ohio aquatic (Scheiring and Foote, 1973; Steinly, 1978), 1984) limnic wrack beds consisted of varying quantities of wet decaying plant material washed onto maritime and lake shores, respectively. Repeated freezing and thawing during spring months uproot aquatic hydrophytes and strong wave action deposits leaves and stems on the shores.

The percent relative abundance (R.A.) of each species within the aquatic habitats was calculated. The percentage is equivalent to the number of a single species divided by the total number of ephydrids within the habitat. The result is multiplied by 100. The percentage ranges (Scheiring and Foote, 1973; Regensburg, 1976; Deonier and Regensburg, 1978; Steinly, 1978; Steinly and Deonier, 1980; Steinly, 1984) were characterized as follows: 1–2% rare (r); 3–8% occasional (occ); 9–14% common (c); 15–25% abundant (a); and 26–100% very abundant (va) (Table 2).

The ephydrid community composition of the marine Scandinavian supra-littoral (watt) and rock pool were compared by means of the Sorenson index of similarity (I) with all marine populations (Table 4). Shore fly population com-

Table 4. Similarity of ephydrid faunas in Scandinavian marine habitats.

Marine Habitats	Index of Similarity (I)	
	Watt	Rock Pool
Watt ¹	—	—
Rock pool ²	0.364	—
Wrack ³	0.316	0.400
Marsh	0.555	0.316
Grass pool ⁴	0.273	0.348
High sand beach	0.258	0.250
Sand pool ⁵	0.240	0.462
Hockenya ⁶	0.462	0.429

¹ Watt equivalent to supralittoral.

² Coastal rock pool adjacent to watt.

³ Decaying rows of plant debris.

⁴ Grass pool within marine marsh.

⁵ Sand pool within high sand beach.

⁶ Terrestrial zone farthest from supralittoral where topsoil largely independent of direct marine effects—permanent macrophytes.

position in all Scandinavian maritime habitats was reported by Dahl (1959). Additionally, the Sorenson index was utilized to compare shore fly populations in aquatic habitats located on the southeastern shore of Lake Erie (Table 5). The value of I ranges from 0 when there is no similarity (no species shared) between habitats to 1 when there is complete similarity (all species shared). The similarity index was calculated with the formula $I = 2C/A B$ where I is the index of similarity, C is the number of species shared, A is the number of species in habitat A, and B is the number of species in habitat B (Scheiring and Deonier, 1979). Ephydrid species numbers (richness values) in marine and freshwater habitats are listed in Table 3.

In Tables 4 and 5, marine and aquatic habitats are listed from frequently to infrequently inundated. The marine watt is inundated by tides and subjected to wave action daily while high sand beach and Hockenya are infrequently flooded by storms. Tidal inundation was negligible on the Lake Erie beaches, but these localities were subjected to extensive wave action when wind velocity was greater than 10 mph. All marine habitats had significant salinity levels; however, salt concentrations were thought to play a minor role as an ecological factor (Dahl, 1959; Hinton, 1976a).

RESULTS

The first comprehensive ecological and distributional investigation of the Ephydridae was accomplished in Scandinavia (Dahl, 1959). Of 68 shore fly species, Dahl recorded 41 species from marine habitats (biotopes). Of the 105 species in northern Ohio (Steinly and Deonier, 1980), 32 ephydrid species were collected in Lake Erie freshwater habitats (Table 2). Examination of habitat shore-fly communities reveals greater species richness (s) in stable Scandinavian marine and Lake Erie habitats (Table 3). The regularly flooded and severely disrupted marine watt (supra-littoral) had the lowest s while the infrequently inundated stable high sand beach yielded the greatest s value. Generally marine and freshwater s values increased with the distance above the supra-littoral.

Table 5. Similarity indices of Lake Erie aquatic habitats.

Habitats	Indices of Similarity		
	Wave Zone-Sand	High Sand Beach	Limnic Wrack
Wave zone-sand	—	—	—
Limnic wrack	0.706	0.555	—
High sand beach	0.736	—	—
Sedge-meadow	0.460	0.370	0.400
Marsh-reed	0.357	0.200	0.222

When marine shore fly communities were compared with the Sorenson index of similarity (I), the lowest I values were generated by the comparison of watt and rock pool to high sand beach. Also, the comparison of watt and rock pool with all marine habitats yielded low I values (Table 4).

The dominant species of Ephyridae in the Lake Erie sedge-meadow were *Scatella favillacea* Loew (va) and *Ephydra riparia* Fallén (a) (Table 2). *E. riparia* was rarely found in marsh-reed habitat. *Hecamedoides glaucellus* (Stenhammar) was collected from high sand beach (va), wave zone (c), and limnic wrack (a) habitats. Additionally, large numbers of *S. favillacea* (va) and *S. obsoleta* Loew (va) were found in the wave zone. Relatively few *S. obsoleta* (r) were collected in other freshwater habitats. *Hydrochasma leucoproctum* (Loew) (a) was dominant in the high sand beach habitat. The dominant shore-fly species in limnic wrack included *S. stagnalis* (Fallén) (va) and *Discocerina obscurella* (Fallén) (a). Large numbers of *S. favillacea* (va) and *S. stagnalis* were collected in the marsh-reed habitat.

The five aquatic Lake Erie habitats were compared with the Sorenson index of similarity (Table 5). The wave zone, high sand beach, and limnic wrack habitats had the greatest similarity. The comparison of sedge-meadow and marsh-reed to wave zone, high sand beach and limnic wrack ephydrid assemblages generated similarity values less than 0.460. Although the habitats within freshwater lake and marine ecosystems were located in close proximity to one another, the relatively low I values suggest that indigenous shore-fly communities were distinct species assemblages. Only the comparison of aquatic wave zone to high sand beach and limnic wrack yielded high indices of similarity.

DISCUSSION

During periodic storms, Scandinavian marine and Lake Erie beaches are subjected to intensive wave action. Additionally, marine beaches are exposed to varying degrees of wave action that depended on daily tides and wind velocity. The severity of substrate disruption has a significant impact on ephydrid nutrient and oviposition resources. Scheiring (1975) proposed that vegetation amount present during the year, the amount of organic debris and species utilizing the organic material, vegetation present at various times of the year, the length of time the vegetation was present and the dominant vegetation species were important habitat resources. Clearly, these nutrient and oviposition resources are disrupted by the physical impact of wave action. In an analysis of Iowa and northeast Ohio lotic habitat characteristics, Scheiring and Deonier (1982) found

shore fly richness variation was accounted for by the abundance and type of vegetation, presence of running water, and frequency of inundation. In all probability, the types and abundance of macroflora and microorganisms found on Lake Erie and marine beaches are limited by severity and frequency of violent inundation. Also, the intensity and frequency of inundation has a direct effect on the survival of ephydrid immature stages. Barton and Hynes (1978a) reported the elimination of wave-zone benthic macroinvertebrate communities by storms. Additionally, Barton and Hynes (1978b) reported that the variety and relative abundance of invertebrates on the exposed shores of the Laurentian Great Lakes were related directly to substratum stability. At more sheltered sites, Evans (1982) observed decreases in micrometazoan densities with depth above (+1 meter) and below (-1 meter) the Lake Erie wave zone. The reverse trend (increasing densities with increasing depth) was found in all wave-zone sites and was attributed to stress imposed on the fauna by wave induced sand-grain movement.

Although Ohio and Iowa lotic habitats have relatively high richness values (s) (Scheiring and Deonier, 1982), Scandinavian marine (Dahl, 1959) and Erie beaches have low s values. Iowa and northeastern Ohio lotic habitats have substrates that retain moisture (Scheiring and Deonier, 1982) while Scandinavian and Lake Erie beaches dry rapidly. Beach habitat (sand and/or rock) substrate is well drained and subject to solar and wind desiccation. In all probability, the movement of substrate and xeric beach conditions precluded the colonization of diverse and abundant macroflora and shore-fly assemblages.

Shore-fly relative abundance values suggest that several species are adapted to the indigenous physical and biological conditions peculiar to Lake Erie habitats (Table 2). *Scatella obsoleta*, *S. stagnalis*, *Ephydra riparia*, *Hydrochasma leuco-proctum*, and *Discocerina obscurella* were found in large numbers in the wave zone, marsh-reed, sedge-meadow, high sand beach, and limnic wrack, respectively.

The total number of marine species confirms that the majority of Scandinavian shore flies are capable of utilizing saline habitats. The distribution of ephydrid species richness-values suggests that frequency and intensity of inundation has a major ecological impact. Scheiring and Deonier (1979) believed resource quantity increased the richness and abundance of well adapted ephydrid species in transient habitats.

In the watt and rock-pool habitats, herbivorous ephydrids had only a few algal species available (Dahl, 1959). Scheiring (1974) analyzed aquatic ephydrid species diversity and evenness in relation to habitat stability and available larval food. Scheiring (1974) and Deonier (1965) concluded that shore-fly larval adaptations are more important than those of adults in the determination of habitat distribution. Simpson (1976) noted marine shore fly larvae required relatively quiescent habitats, where the immature stages were protected from appreciable water movement. Scandinavian marshes were dominated by thick-growing macrophytes and algal populations (Dahl, 1959). Significant quantities of undisturbed organic debris provided ample substrate for micro-organism proliferation. Also, freshwater (= limnic) wrack, composed of decaying organic matter, provided a substrate for micro-organism growth (Scheiring and Foote, 1973). Although the marine wrack habitat is transient, the habitat may provide substantial larval and adult food resources for rapidly developing ephydrid species. Steinly and Runyan (1979) reported rearing the larvae of *Hecamede albicans* (Meigen) on marine mussels

commonly encountered in marine wrack rows. *H. albicans*, utilizing a transient habitat and food supply in the intertidal zone, completed development within ten to fifteen days (Steinly, unpubl.). Also kelp fly species (Dobson, 1976) utilized decaying vegetation in marine wrack. In all probability, kelp flies and *H. albicans* avoid periodic supra-littoral inundation, and the disruption of nutrient resources with a shortened life cycle. *Scatella picea* (Walker) and *Scatella stagnalis* (Fallén), freshwater shore flies encountered in ephemeral mud-shore habitat, have shortened life cycles (Connell and Scheiring, 1982; Foote, 1979). Rapid ephydrid development, a temporal adaptation, allows these species to avoid wave action and/or rapid stream flow associated with storms in marine and freshwater habitats, respectively.

Scandinavian marine grass pool have substantial accumulations of plant fragments and a rich grass vegetation surrounding and within the depressions (Dahl, 1959). The maritime high sand beach has diverse macrophyte and micro-organism populations. Species of diatom, chlorophyte, cyanophyte algae, and bacteria were commonly found by Dahl (1959). Marine sand-pool habitat had no permanent macrophytic vegetation but was bordered by highly productive algae populations (Dahl, 1959). These relatively stable habitats were infrequently inundated and were populated by a diverse and/or abundant micro-flora. Stable habitat substratum and nutrient resources probably have a significant influence on increased ephydrid s values.

The data compiled in Table 1 and the text suggest that more than half of the marine insect species are confined exclusively to sheltered habitats. In all probability, quiescent marine and freshwater habitats provide a refuge from severe wave action. In particular, saltmarsh, grass pool, marine high sand beach, sand pool, marsh-reed, and sedge-meadow insects have available a greater number of stable niches and nutrient sources.

Habitat preferences of marine and lake shore insects and behavioral and temporal adaptations of intertidal insect species substantiates the importance of avoiding intensive wave action. Additionally, the species richness distribution patterns, similarity, and relative abundance indices associated with Scandinavian marine and/or Lake Erie ephydrid populations support the wave disruption theory.

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TWO NEW SPECIES OF WATER-STRIDERS OF THE GENUS *OIOVELIA*
FROM THE TEPUI CERRO DE LA NEBLINA,
VENEZUELA (HEMIPTERA: VELIIDAE)

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Abstract.—Two new species of veliid water-striders, *Oiovelia spumicola* and *Oiovelia rivicola*, from Venezuela are described; distinctive characters are illustrated with pen and ink line drawings and SEM micrographs. For *O. spumicola* the unusual color and the unusual habitat in piles of foam on tropical blackwater streams are discussed. A key to identify the three species now known in the genus *Oiovelia* is included. New and additional illustrations and new distribution records for the type species of the genus, *O. cunucunumana* Drake and Maldonado Capriles, are provided.

The genus *Oiovelia* and the one included species *O. cunucunumana*, based on three female specimens from Venezuela, were described by Drake and Maldonado Capriles (1952); later, a winged male from Paraguay was described as the "allotype" by Drake and Roze (1955). The genus was not reported again until Andersen (1982) included it in his key to the genera of the Veliinae.

The two new species described below were collected during an expedition to Cerro de la Neblina, the "Mountain of the Mists," in the Territorio Federal de Amazonas, Venezuela, at the Brazilian border. Cerro de la Neblina is one of the numerous mesas (tepui)s which are eroded sandstone remains of the Guiana Highland Shield, a former large plateau which probably dates back to the time when South America and Africa formed a single huge continent. The tepuis are home to numerous endemic genera of plants and some animals. Although the genus *Oiovelia* occurs on Cerro de la Neblina, it is not restricted to the tepuis because I have seen specimens of *O. cunucunumana* from Venezuela, Brazil, Paraguay and Peru in the entomological collections of the National Museum of Natural History, Smithsonian Institution.

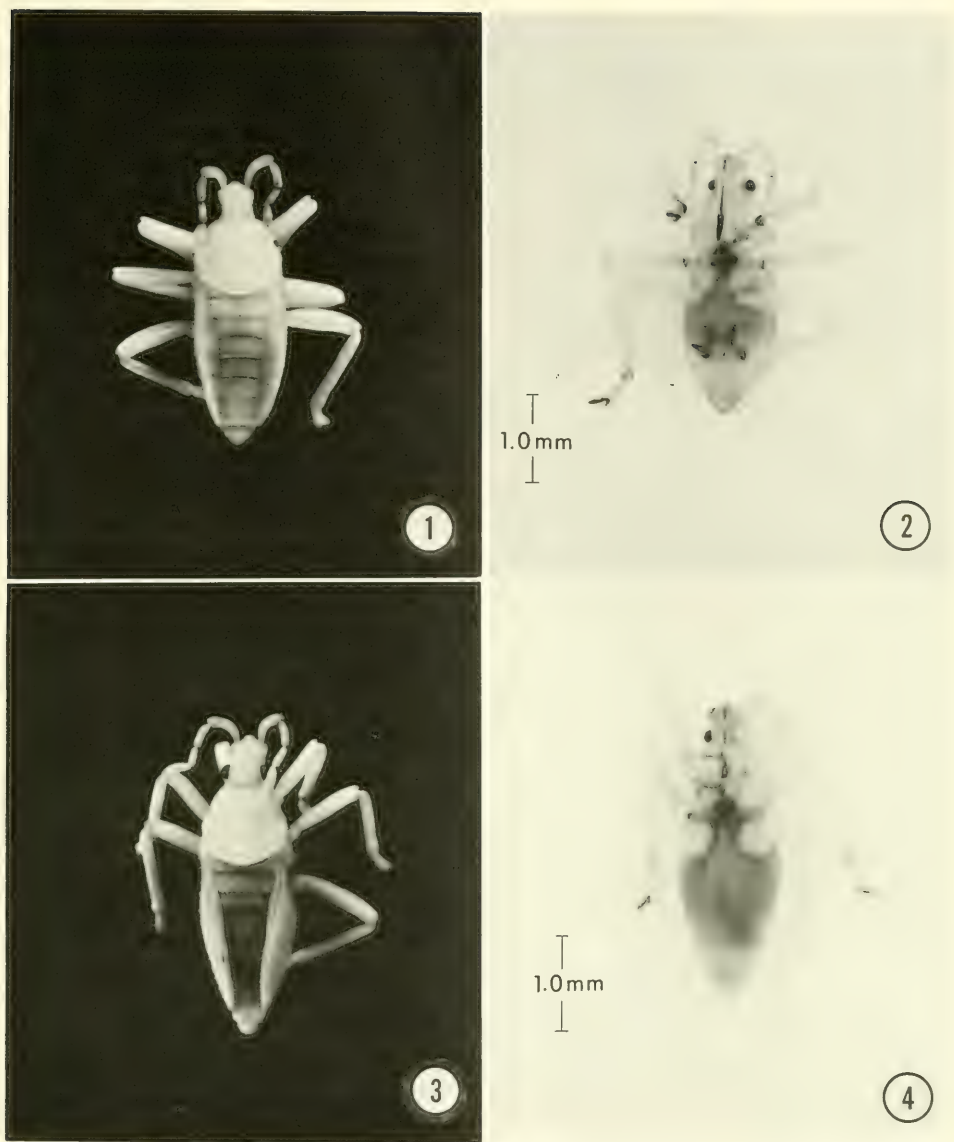
The new species *O. spumicola* is interesting because it is the only veliid known that lives on and in piles of foam on blackwater streams. All nymphs and apterous adults collected are creamy white; therefore, the specimens matched the color of the foam and were difficult to see. The few winged adults were grey and more obvious on the white foam. However, if the winged forms disperse the species by flying to new habitats, their darker color over the blackwater streams and the forest floor would make them less obvious to predators.

***Oiovelia spumicola*, NEW SPECIES**

Figs. 1-12, 21

Apterous holotype male.—*Size*: Length, 3.01 mm; greatest width, 0.97 mm.

Color: Creamy white except (Figs. 1-4): eyes reddish brown; apical third of



Figs. 1–4. *Oiovelia spumicola*, new species. 1, Male, dorsal view. 2, Male, ventral view. 3, Female, dorsal view. 4, Female, ventral view.

rostrum dark brown; antennal segments 1 and 2 brownish yellow, last segment creamy yellow; apicomedial edge of protibiae, apices of last tarsal segments, and tarsal claws brownish yellow; mid-metasternum black. With a rather broad medial, V-shaped, dark reddish-brown structure visible through the cuticle of sterna 4 and 5 (Fig. 2).

Head: Width between eyes, 0.35 mm. Cuticle finely pubescent; with few long, slender, light yellowish-brown setae above and in front of eyes (Fig. 5). Rostrum extending to mesocoxae. Antennae (Fig. 6) with fine, dense, yellowish pubescence and a few longer, darker setae interspersed; segment 1 arcuate, distinctly swollen apically, distinctly thicker than and twice as long as segment 2; segment 2 more

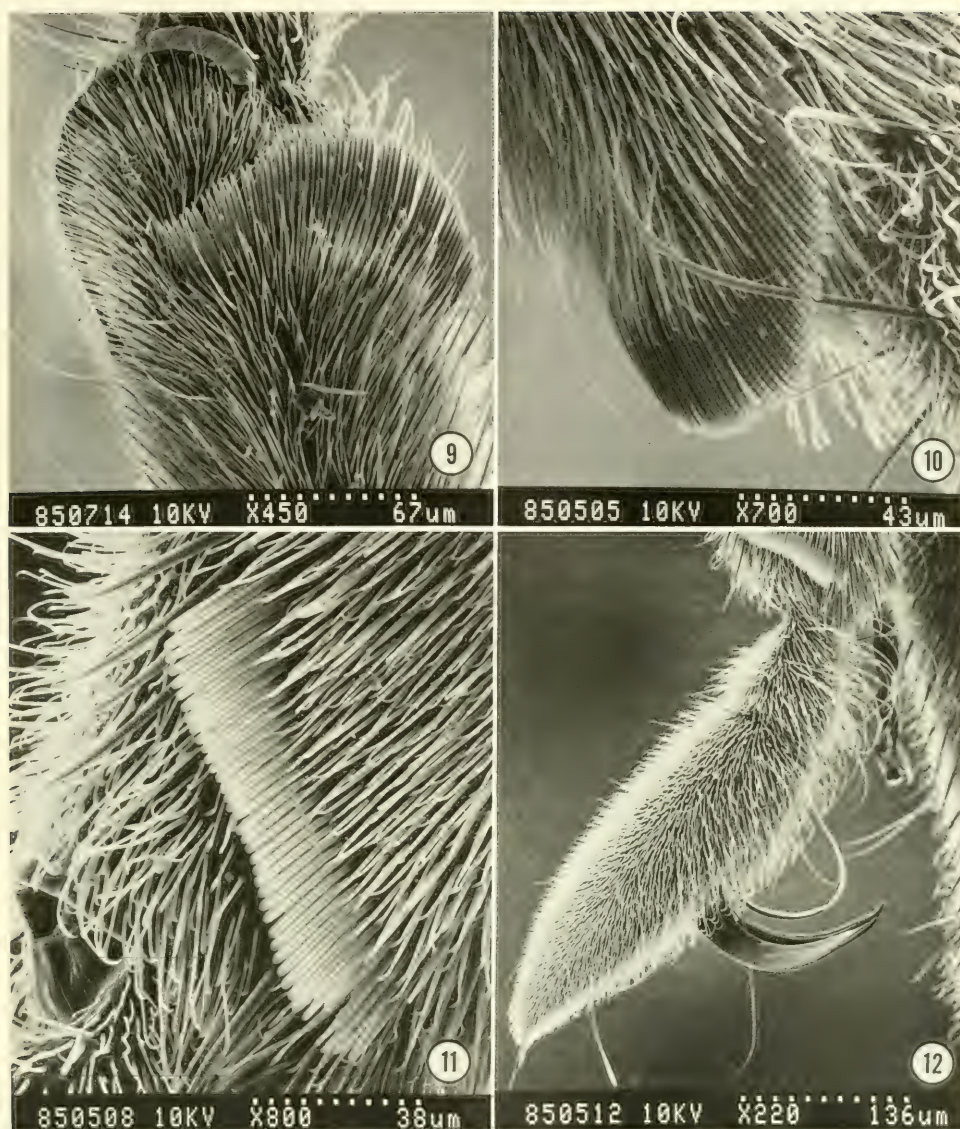


Figs. 5–8. *Oiovelia spumicola*, new species. 5, Head and pronotum, dorsal view. 6, Antenna. 7, Protibial apex. 8, Protibial apex enlarged, ventral view.

slender and slightly longer than segment 3; segment 4 swollen and about a fourth longer than segment 3.

Thorax: Pronotum (Fig. 5) narrowest apically; sides diverging and rounded from shallow constriction at anterior third; midline impunctate; posterior three-fourths coarsely, sparsely punctate; a few coarse punctures laterad of procoxae. Protibia (Figs. 7–11) with a long transverse grooming comb, a short transverse grooming comb, and a distal short arcuate grasping comb.

Abdomen: Cuticle with fine, dense, short, yellowish pubescence. Laterotergites strongly reflexed above abdominal terga. Last segment with ovate genital capsule twice as long as seventh segment on midline.



Figs. 9–12. *Oiovelia spumicola*, new species. 9, Protibial apex with grasping comb and long grooming comb. 10, Long grooming comb. 11, Short grooming comb. 12, Tarsal claws.

Male genitalia: Proctiger convex; with a single toothlike process on dorsal surface. Clasper narrow at base, widest slightly before midlength; tapered distally and ending as a small, acute, apical hook as illustrated (Fig. 21).

Apterous allotype.—Length, 3.24 mm; greatest width, 0.97 mm. Female genital capsule about as long as seventh segment on midline. Otherwise, similar in appearance to the holotype male.

Winged males.—**Size:** Length, 3.24 to 3.44 mm; greatest width, 1.35 to 1.39 mm.

Color: Dorsum of head, antennal segments 1–3, sides of thorax, and sides of abdominal sterna dark brown. Abdominal sterna 4 and 5 with a rather broad, medial, V-shaped, dark reddish-brown structure showing through cuticle. Prono-

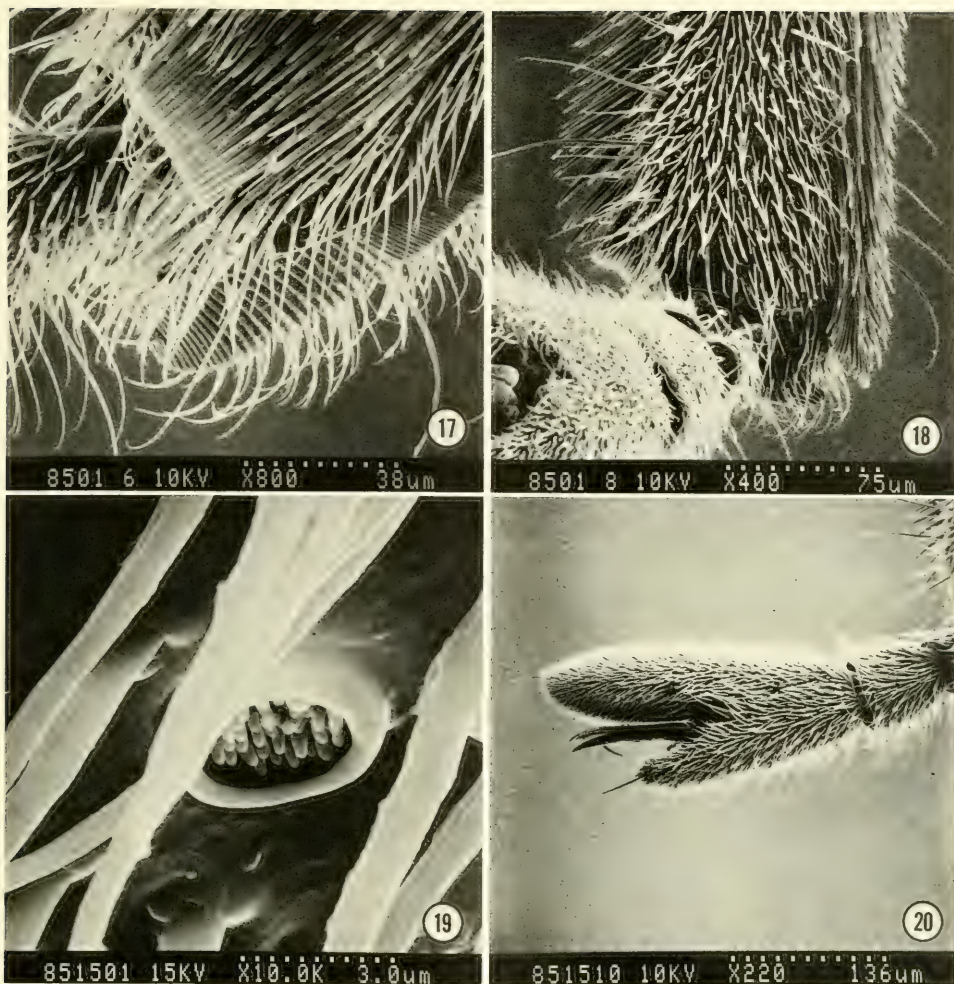


Figs. 13–16. *Oiovelia rivicola*, new species. 13, Head and pronotum. 14, Head. 15, Protibia. 16, Protibial apex.

tum with anterior third reddish brown and posterior two-thirds creamy yellow. Legs creamy yellow except apices of femora, bases of protibiae, mesotibiae, and metatibiae and tarsal segments dark brown. Forewing dark brown except Sc + R creamy yellow.

Head: Similar to apterous form except median longitudinal groove on head more distinct.

Thorax: Similar to apterous form except pronotum diverging strongly to mid-



Figs. 17–20. *Oiovelia rivicola*, new species. 17, Protibial apex. 18, Protibial apex showing peg-plates. 19, Peg-plate enlarged. 20, Last segment of tarsus.

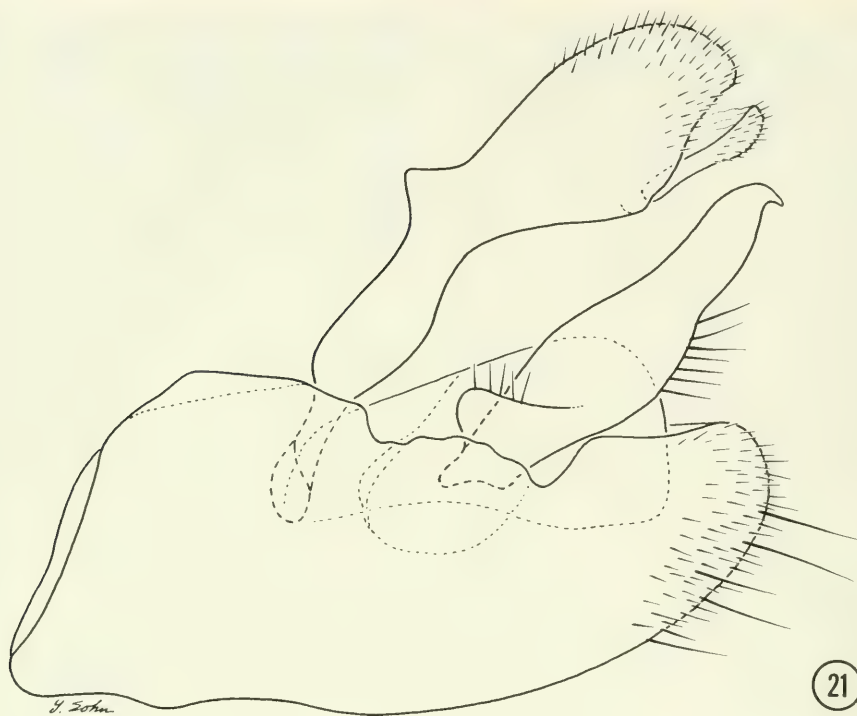
length then becoming strongly angular before converging to rounded base; surface with an occasional long, dark brown seta. Forewing with veins and 4 cells present but obscured by dark brown coloration.

Abdomen: Similar to apterous form but pubescence not as distinctly yellow because of dark cuticular coloration. Genital capsule twice as long as seventh segment on midline as in apterous male.

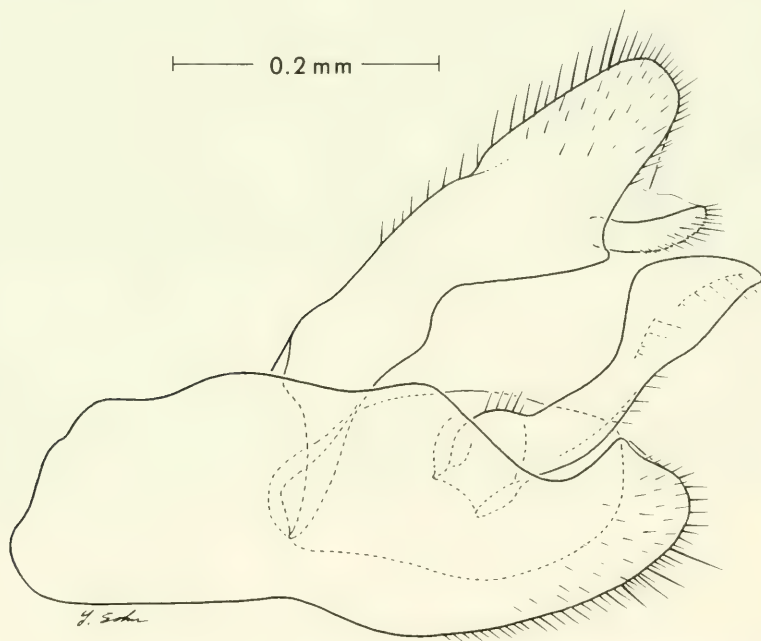
Winged females.—Length, 3.74 to 3.78 mm; greatest width, 1.43 to 1.50 mm. Similar to winged male except genital capsule about as long as seventh segment on midline.

Eggs.—Most of the females were gravid and the eggs are visible through the distended body wall. One female was dissected and three elongate eggs were found packed tightly in the abdomen. The eggs average 0.99 mm in length and 0.42 mm across the diameter; the chorion appears smooth.

Variations.—The only variations noted were in the intensity of the brownish



— 0.2 mm —



Figs. 21, 22. 21, *Oiovelia spumicola*, new species; male genitalia, lateral view. 22, *Oiovelia rivicola*, new species; male genitalia, lateral view.

yellow present on the apterous specimens. The winged forms also vary in intensity of coloration; one specimen has the abdominal sterna creamy yellow instead of dark grey as in the other specimens. Males may be distinguished from females by a broad, dark, almost black, V-shaped structure visible through the cuticle on the middle of the fourth and fifth abdominal sterna (more easily seen when specimens are in alcohol). In a few specimens this structure is very light but the lateral margins are visible.

Comparative notes.—The wingless specimens of *O. spumicola* differ from specimens of *O. rivicola*, n. sp., and *O. cunucunumana* Drake and Maldonado Capriles (1952) by the creamy yellow integument. The winged form of *O. spumicola* may be distinguished immediately from specimens of *O. rivicola* and *O. cunucunumana* by the creamy yellow legs. Male genitalia of *O. spumicola* have less sinuate claspers with few (6 or 7) long setae on the middle third posteriorly; the apex is acute and slightly hooklike; also, the proctiger has a single moderately broad dentiform process dorsally at midlength (Fig. 21). In contrast, males of *O. rivicola* have the claspers narrowed at the base and diverging to a broad apex (Fig. 22); the proctiger lacks toothlike processes on the dorsal surface. Males of *O. cunucunumana* have sinuate claspers with short setae on the posterior margin except at the basal fourth; the apex is bluntly rounded (Fig. 25); and the proctiger lacks a dorsal, dentiform process at midlength (Fig. 25).

Type-date.—Apterous holotype male: VENEZUELA, Territorio Federal Amazonas, Cerro de la Neblina, Camp XI, 00°52'N, 65°58'W, 27–28 February 1985, 1450 m, P.J. and P.M. Spangler, R.A. Faitoute; deposited in the National Museum of Natural History, Smithsonian Institution. Apterous allotype, same data as holotype. Paratypes: Same data as holotype, 33 apterous and 3 winged males; 40 apterous and 2 winged females. In addition, 52 nymphs were collected with the type specimens but are not designated as paratypes. Paratypes will be deposited in the collections of: The Instituto de Zoología Agrícola, Facultad de Agronomía, Maracay, Venezuela; the British Museum (Natural History), London, England; The Snow Entomological Museum, University of Kansas, Lawrence, Kansas; the Zoological Museum, University of Copenhagen, Copenhagen, Denmark; Laboratorium voor Zoologische, Oecologie en Taxonomie, Utrecht, Netherlands; and the collection of John T. Polhemus, Englewood, Colorado.

Etymology.—The specific epithet *spumicola* was formed by combining the following. *L. spuma*, meaning “foam”; with *L. cola*, meaning “dweller in”; in reference to the curious habitat in which this species was found.

Habitat.—The creamy white specimens described above were first noticed as they were feeding on a dead, adult black stonefly which was floating in a pile of foam in an eddy of a small stream. When the stonefly was collected, the veliids scurried over the surface and into the foam. Further observations on this curious behavior led to the conclusion that piles of foam apparently are their normal habitat. Undisturbed specimens would wander in and out of the foam presumably searching for other organisms trapped in it.

Most specimens were collected by dipping up piles of foam in a net and rinsing the foam through the mesh; this left the veliids in the net. A few specimens were aspirated from the surface of the foam and a few were found in leaf packs against which the foam had drifted. Their creamy white color blended closely with the

foam but contrasted sharply against the dark green and brown leaves in the leaf packs which suggests that the light color is a protective adaptation for these foam-inhabiting veliids. All the nymphs and apterous adults are creamy white and only the five winged adults are darker as described above but they are lighter colored than most veliids.

Oiovelia rivicola NEW SPECIES

Figs. 13–20, 22

Macropterous holotype male.—*Size*: Length, 3.16 mm.; greatest width, 1.04 mm.

Color: Head reddish brown; eyes black and shiny; antennae dark reddish brown. Pronotum reddish brown as head and a broadly V-shaped somewhat silvery macula on basal fourth. Apical third and ventral surface of rostrum (in repose), dark brown; other parts brownish yellow. Legs dark reddish brown except coxae and trochanters brownish yellow. Venter dark reddish brown; with small, indistinct, longitudinal, band-like maculae on dorsolateral margins of metasternum; band-like maculae on dorsolateral margins of all abdominal sterna.

Head: Width between eyes, 0.23 mm. Cuticle with fine pubescence (Figs. 13, 14); with numerous long, slender, dark reddish-brown setae in front of eyes and a few between eyes. Rostrum extending to mesocoxae. Antennae with fine, dense, reddish-brown pubescence; a few longer, darker setae interspersed on last two segments; segment 1 arcuate, gradually swelling toward apex, slightly thicker and slightly longer than segment 2; segment 2 more slender and slightly longer than segment 3; segment 4 swollen and slightly longer than segment 3.

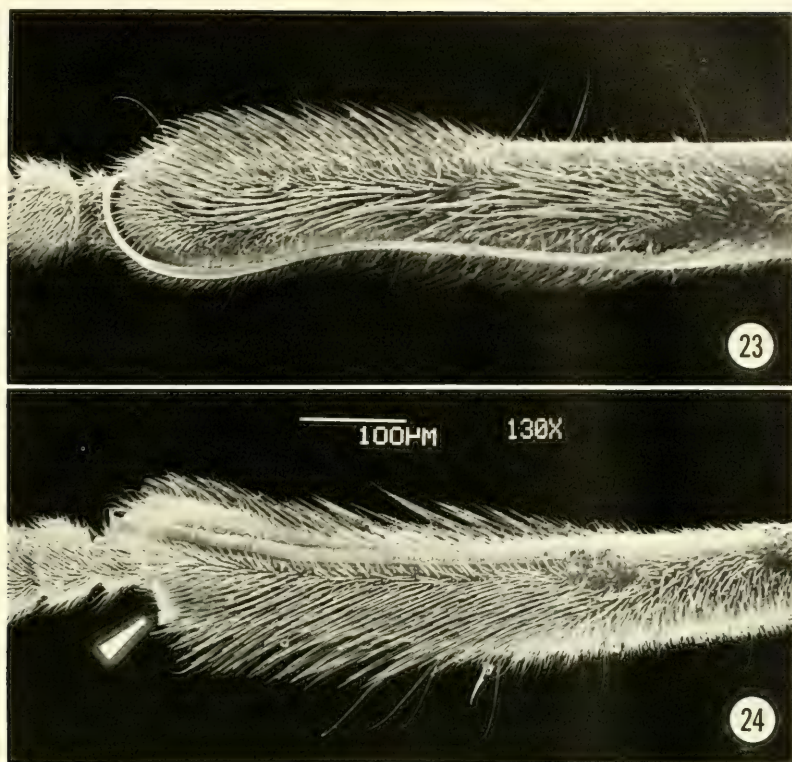
Thorax: Pronotum (Fig. 13) narrowest apically; sides diverging and gibbous behind shallow constriction at anterior third; disk coarsely, sparsely punctate except on midline, punctures more obvious in constricted area; with an oblique row of coarse, distinct punctures laterad of procoxae. Protibia (Figs. 15–18) with long, grasping comb (Fig. 15) extending about two-thirds length of tibia and a grooming comb distally (Figs. 16, 17, arrow); lower surface (Figs. 18, 19) with peg-plates. Last segment of protarsus typically expanded (Fig. 20). Forewing as long as abdomen; with short, narrow, longitudinal, white macula at base beside pronotal lobe.

Abdomen: Cuticle with fine, dense, short, yellowish pubescence. Laterotergites strongly reflexed above abdominal terga. Last segment with ovate genital capsule a third longer than seventh segment on midline.

Male genitalia: Proctiger convex without toothlike processes on dorsal surface. Clasper narrow at base and diverging to broad apex as illustrated (Fig. 22).

Macropterous allotype.—Similar to male except: Length, 3.40 mm; greatest width, 1.20 mm. Coarse pronotal punctures dense and more obvious than those on male. Forewings as on male. Female genital capsule about a fifth longer than seventh abdominal segment on midline.

Variation.—This new species varies in the intensity of the silvery maculae on the pronotum. When wet, the maculae are indistinct but become more obvious as the cuticle dries. On some specimens a partial, longitudinal silvery stripe is present on the midline. Also, on some specimens the abdomen is yellowish brown with a narrow, black, band-like area above the lateral, shiny, elongate, cuticular depressions; in other specimens the abdomen is almost entirely black which ob-

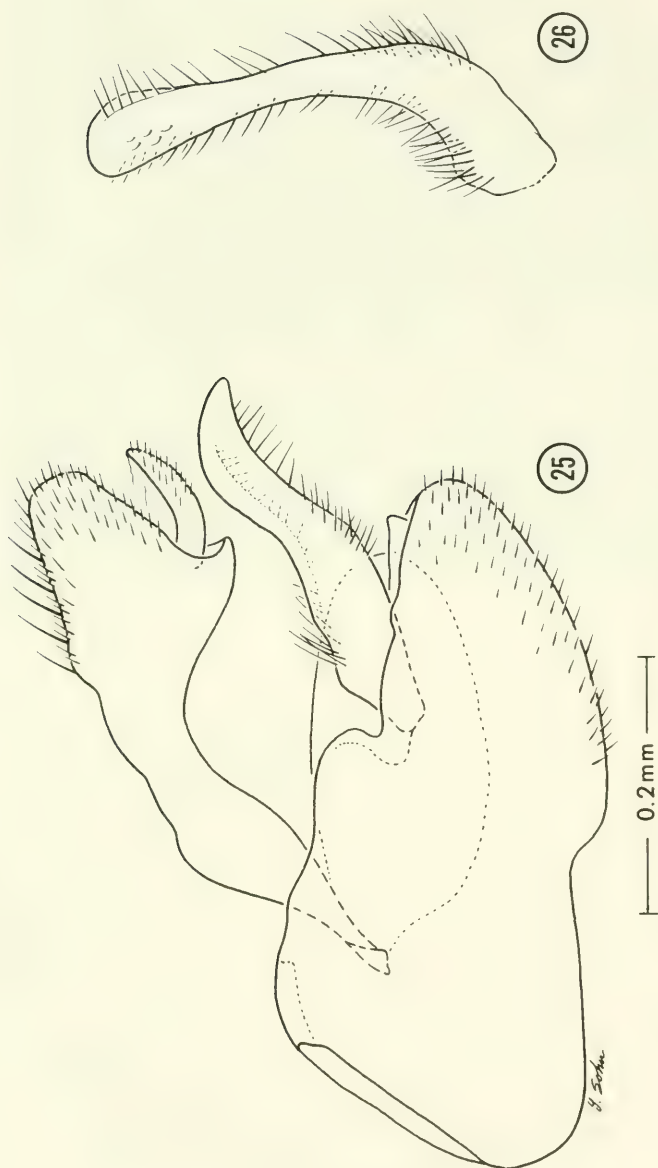


Figs. 23, 24. *Oiovelia cunucunumana* Drake and Maldonado Capriles. 23, Protarsal grasping comb. 24, Protarsal grasping comb and grooming comb (arrow).

scures the band-like area. Females are more robust and are longer (3.66–3.89 mm) than the slender and shorter males (3.16–3.32 mm).

Comparative notes.—The new species *O. rivicola* most closely resembles *O. cunucunumana* Drake and Maldonado Capriles (1952) but may be distinguished from that species by the following combination of characters: 1, apical segment of antenna only slightly broader than preapical segment instead of a third broader; 2, body more slender and shorter (length, 3.16 vs. 4.4 mm); 3, narrow black band-like maculae on dorsolateral margin of metasternum and abdominal sterna above the shiny, elongate, cuticular depressions; 4, in males, the clasper strongly broadened preapically (Fig. 22) instead of simply sinuous (Fig. 25).

Type-data.—Macropterous Holotype Male: VENEZUELA, Territorio Federal Amazonas, Cerro de la Neblina, base camp, 140 m, 0°50'N, 66°10'W, 21 February 1985, P. J. & P. M. Spangler, R. A. Faitoute, & W. E. Steiner; deposited in the National Museum of Natural History, Smithsonian Institution. Macropterous allotype, same data as holotype. Paratypes: Same data as holotype, 15 males, 9 females; same data except 24 February 1985, 7 males, 4 females. Paratypes will be deposited in the Universidad Central de Venezuela, the British Museum (Natural History), the University of Kansas, and the collection of John T. Polhemus, Englewood, Colorado.



Figs. 25, 26. *Oiovelia cunucunumana* Drake and Maldonado Capriles. 25. Male genitalia, lateral view, with clasper in situ. 26. Clasper detached from capsule.

Etymology.—The specific epithet *rivicola* was formed by combining the following. *L. rivus*, meaning “stream or brook”; with *L. cola*, meaning “dweller in”; in reference to the presumed habitat of this species.

Habitat.—All specimens were attracted to and collected at an ultraviolet light operated at base camp near the Rio Baria.

***Oiovelia cunucunumana* Drake and Maldonado Capriles**

Figs. 23–26

Oiovelia cunucunumana Drake and Maldonado Capriles, 1952:52.—Drake and Roze, 1955:107.

This was the only species described for their new genus *Oiovelia*. The description was based on a winged female holotype and two winged female paratypes. Later, when both sexes became available from Paraguay, Drake and Roze (1955) described a winged male as the allotype.

The length of *O. cunucunumana* was not given for the holotype nor allotype in the articles cited above; the length for each is: holotype, 3.86 mm; allotype, 3.39 mm.

The grasping comb (Figs. 23, 24) on the male protarsus mentioned by Drake and Roze (1955) and the short, transverse, grooming comb (Fig. 24, arrow) are illustrated here from the male from Nova Teutonia, Brazil. The genitalia of the male allotype from Paraguay were dissected, cleared, and are illustrated (Fig. 25). Because the clasper is different in shape when drawn laterally in situ (Fig. 25) than when detached, it is drawn separately to illustrate the difference (Fig. 26).

Type specimens, examined.—Holotype: VENEZUELA: Territorio Amazonas, mouth Cunucunuman R., 3 April 1950, J. Maldonado Capriles, 1 winged female. Allotype: PARAGUAY: Paraguay R., 25 Nov. 1951, 1 male. Paratype: VENEZUELA: Territorio Amazonas, Culebra, N. Duida, 1–4 July 1950, J. Maldonado Capriles, 1 female. The specimens cited above are in the collections of the U.S. National Museum of Natural History (NMNH), Smithsonian Institution. However, a second female paratype reported by Drake and Maldonado Capriles (1952) from the same locality as the holotype and another specimen reported by Drake and Roze (1955) from “a small stream near Caracas, Venezuela” are not among the specimens in the NMNH.

Additional specimens examined (NMNH).—BRAZIL: Nova Teutonia, 8 July 1963, F. Plaumann, 1; Santa Catarina, 5 Feb. 1950, F. Plaumann, 1 male, 1 female. PARAGUAY: Paraguay R., 25 Nov. 1951, 6 females; same locality, 28 Nov. 1951, 1 female. PERU: Iquitos, Amazon River, 12 Oct. 1955, S. S. Roback, 1 female. The specimens from Paraguay and Venezuela were identified by C. J. Drake; the single female from Peru was identified by J. C. Lutz.

KEY TO SPECIES OF *OIOVELIA*

1. Pronotum entirely creamy yellow (wingless forms) or only on posterior half (winged forms); with only a few additional long brownish setae on anterior fourth. Antennae densely tomentose (Fig. 6), brownish yellow except last segment creamy yellow (wingless forms). Femora creamy yellow except narrowly brownish yellow apically. Clasper of male genitalia ta-

- pered distally, ending in acute, apical hook (Fig. 21) *spumicola*, new species
- Pronotum reddish brown; with numerous, long, dark brown setae; setae abundant on anterior third and along margins but sparse on discal area. Antennae not densely tomentose (Figs. 13, 14). Femora reddish brown. Clasper of male genitalia not hooked (Figs. 22, 25) 2
2. Ratio of antennal segments 31:27:19:22. Total length, 3.16–3.89 mm. Clasper of male genitalia broadened preapically (Fig. 22) *rivicola*, new species
- Ratio of antennal segments 30:22:15:19. Total length, 3.39–3.97 mm. Clasper of male genitalia not broadened apically when viewed in situ (Fig. 25) but broadened when seen detached (Fig. 26) *cunucunumana* Drake and Maldonado Capriles

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In addition, I thank the following people for their assistance: Phyllis M. Spangler, Robin A. Faitoute, and Warren E. Steiner for assistance with collecting and preparing the specimens of these new species for study; Dr. R. C. Froeschner for helpful discussions and suggestions; Young T. Sohn, biological illustrator, for the pen and ink drawings; the administrators of the Smithsonian Institution’s Scholarly Research Fund for supporting the fieldwork during which these new veliids were collected; and Phyllis Spangler for typing the manuscript into the word processor.

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HOST SPECIFICITY OF *OCHRIMNUS MIMULUS* (STÅL)
(HEMIPTERA: LYGAEIDAE) WITH NOTES ON ITS PHENOLOGY

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Abstract.—*Ochrimnus mimulus*, a seed feeding bug infesting *Baccharis halimifolia* and *B. neglecta*, was studied to determine its host specificity. Laboratory tests indicated that it would oviposit in a wide range of asteraceous inflorescences. When early instar nymphs were placed on inflorescences in a no-choice experiment some individuals fed more than four days on *Solidago altissima* and *Chrysanthamnus nauseosus* and one individual was reared through to an adult on *Conyza canadensis*. In the field, nymphs were found in the inflorescences of *S. altissima* at two sites in Texas. It was therefore concluded that *O. mimulus* was not sufficiently specific to introduce into Australia for the biological control of *B. halimifolia*.

Ochrimnus mimulus (Stål) is a small lygaeid bug frequently found in large numbers on the inflorescences of *Baccharis halimifolia* L. and *B. neglecta* Britton (Asteraceae: Astereae). Although it is represented in most major insect collections in the United States, little is known of its host range, biology, or phenology. Blatchley (1926) recorded it from the heads and stems of thistles and Brailovski (1982) listed *B. halimifolia* and *Taxodium distichum* (L.) (Taxodiaceae) as hosts.

The genus *Ochrimnus* Stål is mainly Neotropical and contains 43 species, most of which are associated with the inflorescences of various asteraceous plants (Brailovski, 1982). Adults of some species have been collected on non-asteraceous plants. *Ochrimnus collaris* (Fabricius) has been collected frequently on *Pisonia "albida"* (Wolcott, 1936, 1941; Ramos, 1946). *Zea mays* L. has been suggested as a possible host for *O. pallescens* (Stål) (Gibson and Carillo, 1959). Nymphs of *O. pallescens* and *O. pallidocinctus* (Stål) have been collected on plants from more than one tribe of the Asteraceae (Brailovski, 1982). Six species have been recorded from *Baccharis* spp. Five associations recorded by Brailovski (1982) are: *O. mimulus* from *B. halimifolia*; *O. carnosulus* (Van Duzee) and *O. chontalensis* (Distant) from *B. trinervis* (Lam.); *O. foederatus* (Van Duzee) from *B. sarathroides* Gray and *O. barberi* (Slater) from *B. glandulosa*. More recently, North American Field Station staff have collected *O. lineoloides* (Slater) from *B. braunii* (Polak) in Costa Rica.

The primary purpose of this study was to determine by either field or laboratory studies whether this insect might breed on any non-*Baccharis* plants. A significant indication that it might breed on non-*Baccharis* species would lead to its rejection as a biocontrol agent for *B. halimifolia* which is now a serious noxious weed in

Table 1. Number of eggs deposited by *Ochrimnus mimulus* in inflorescences of various plant species.

Plant	Tribe	Mean No. of Eggs
(1) First Experiment		
<i>Baccharis neglecta</i> Britton	Astereae	43
<i>Conyza canadensis</i> (L.) Cronq.	Astereae	6
<i>Haplopappus tenuisectus</i> (Green) Blake	Astereae	12
<i>Solidago altissima</i> L.	Astereae	24
<i>Isocoma wrightii</i> (Gray) Rydb.	Astereae	1
<i>Gutierrezia microcephala</i> (DC.) Gray	Astereae	0
<i>Helianthus annuus</i> L.	Heliantheae	0
<i>Xanthium strumarium</i> L.	Heliantheae	0
<i>Parthenium hysterophorus</i> L.	Heliantheae	13
<i>Zinnia elegans</i> Jacq.	Heliantheae	0
<i>Lactuca sativa</i> L.	Lactuceae	10
<i>Lantana camara</i> L.	Verbenaceae*	0
(2) Second Experiment		
<i>Baccharis neglecta</i> Britton	Astereae	17
<i>Aster novae-angliae</i> L.	Astereae	0
<i>Grindelia squarrosa</i> (Pursh) Dunal.	Astereae	0
<i>Chrysothamnus nauseosus</i> (Pallas) Britton	Astereae	4
<i>Gymnosperma glutinosum</i> (Spreng.) Less.	Astereae	0
<i>Ambrosia trifida</i> L.	Heliantheae	1
<i>Tagetes lucida</i> Cav.	Tageteae	0
<i>Chrysanthemum moriflorum</i> Ramat.	Anthemideae	0
<i>Artemisia frigida</i> Willd.	Anthemideae	20
<i>Gomphrena globosa</i> L.	Amaranthaceae*	0

* Family.

southeastern Queensland and northeastern New South Wales, Australia, and for which biological control agents are now being sought in North America.

NOTES ON DISTRIBUTION, PHENOLOGY, AND BIOLOGY

Ochrimnus mimulus occurs on both *B. halimifolia* and *B. neglecta*. It has been commonly collected from Texas to Florida (Slater and Baranowski, 1978). The following observations were made by inspecting *B. neglecta* in Texas over a three year period. Adults are found on stems almost throughout the year and have even been observed inhabiting old galleries of stem-boring insects inside the stem. They are abundant in early spring (April–May) but, when flowering commences in late September, are found in far greater numbers. Mating occurs on the plant and eggs are laid in the female inflorescences. Development of the nymphs coincides with the duration of flowering and seed development so that when the seeds begin to disperse in late autumn, late instar nymphs and newly molted adults are present. Nymphs can also be found in the soil at the base of the plant at that time. Little is known of their biology in winter, spring and summer when *Baccharis* is not in flower although they appear to overwinter as nymphs and adults.

In the laboratory, adults mated readily in cages and appeared to feed on sugar solutions when these were supplied. Dissection of females revealed an average of 14 immature eggs. Eggs were laid among the flowers within the inflorescence.

Table 2. Number of *Ochrimnus mimulus* nymphs surviving after 4 days and the number completing their development after ten early instar nymphs were placed on inflorescences of various plant species.

Plant	Total Number Surviving 4 Days	Total Number Becoming Adults
<i>Baccharis neglecta</i> Britton	3	1
<i>Solidago altissima</i> L.	0	0
<i>Conyza canadensis</i> L.	5	1
<i>Chrysothamnus nauseosus</i> (Pallas) Britton	5	0
<i>Parthenium hysterophorus</i> L.	0	0
<i>Artemisia frigida</i> Willd.	0	0

They were milky white and elongate with average dimensions of 1.2 × 0.3 mm. Nymphs were observed to insert their stylets through the bracts surrounding the flower and were also observed feeding on the bodies of dead *O. mimulus*.

HOST SPECIFICITY TESTING

Oviposition.—Two experiments were conducted to determine the host specificity of oviposition. In each experiment, eleven or twelve bouquets of the inflorescences of different plant species were placed in a 37 × 27 × 17 cm plastic cage together with two sugar water wicks and approximately 20–40 adult unsexed *O. mimulus* which had been collected from *B. neglecta* growing near Temple, Texas. After 8–9 days when most of the insects had died, the inflorescences were carefully dissected and any eggs counted. Each experiment was replicated twice.

Results (Table 1) show that *O. mimulus* oviposited on quite a wide range of plants in this laboratory experiment. They oviposited on a number of species within the Astereae tribe and on *Ambrosia trifida* and *Parthenium hysterophorus* of the Heliantheae, *Artemisia frigida* of the Anthemideae and perhaps more importantly *Lactuca sativa* of the Lactuceae. They did not oviposit on the non-asteraceous species.

Feeding by nymphs.—Early instar nymphs were collected by sweeping *B. neglecta*. Ten nymphs were placed in each of six petri dishes together with an inflorescence of one plant species. These species flower asynchronously so the material used was of varying maturity and, possibly, quality. The plant material was changed every second day.

Results (Table 2) show that after 4 days there were no survivors on plants selected from outside the Astereae tribe but that nymphs survived on species of three genera within that tribe. A number of nymphs continued feeding on *Conyza canadensis* for quite some time and one individual completed its immature development to become an adult after feeding for about a month.

This very small, exploratory experiment should be interpreted as a demonstration that *O. mimulus* can complete its development in the laboratory on a non-*Baccharis* host. As *Ochrimnus* are considered quite difficult to rear in the laboratory (R. Baranowski, pers. comm.), it would not be at all surprising if *O. mimulus* could develop on some of the other plant species used in this test, were techniques to be refined.

Field survey.—Asteraceous plants were closely examined at a number of sites where *Baccharis* was growing. Both adults and nymphs were found on *S. altissima*

at both Lake Stillhouse Hollow, near Temple, and Conroe, Texas, indicating that *O. mimulus* breeds in *Solidago* as well as *Baccharis*. However, as the insect was much less numerous on the *Solidago* than on the *Baccharis* at these sites, it was evident that *Baccharis* is the preferred host.

DISCUSSION

The investigation showed that although *Baccharis* spp. are the principal hosts, *O. mimulus* also breeds in the field on *Solidago altissima*. Laboratory testing indicated that *Conyza canadensis* might also be a possible host. It therefore appears that this insect is stenophagous and confined to various *Asteraceous* species. It might also be possible that *O. mimulus* has an alternate, spring flowering host as Blatchley (1926) recorded both adults and nymphs on thistles in April in Florida.

Unfortunately, because both *S. altissima* and *C. canadensis* have been introduced into Australia from North America, this insect could not be recommended for introduction into Australia even though it is most unlikely that it would damage any economically important species in that continent.

ACKNOWLEDGMENTS

I thank James A. Slater of the University of Connecticut and Richard M. Baranowski of the University of Florida for their advice on this insect. Identifications were provided by Thomas J. Henry (adults) of the Systematic Entomology Laboratory in Washington, D.C., and R. Baranowski (adults and nymphs).

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**TWO NEW SPECIES OF THE PREDACEOUS MIDGE GENUS
CLASTRIEROMYIA FROM URUGUAY WITH A NEW RECORD OF
C. SCHNACKI FOR ARGENTINA (DIPTERA: CERATOPOGONIDAE)**

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Abstract.—The pupa, male, and female of *Clastrieromyia dycei*, new species, and the female of *C. uruguayensis*, new species, both from Uruguay, are described and illustrated. A key is presented to separate them from the two previously known species of this palpomyiine genus. The male and pupa of *Clastrieromyia* are described for the first time. *C. schnacki* Spinelli and Grogan is recorded for the first time from Argentina.

Spinelli and Grogan (1985) proposed the genus *Clastrieromyia* for two species, *C. schnacki* Spinelli and Grogan, the type-species, from Ecuador, and *C. kremeri* Spinelli and Grogan, from Amazonas, Brazil. They also compared *Clastrieromyia* with all of the other genera in the tribe Palpomyiini.

In this paper we describe two new species of *Clastrieromyia* recently collected in Uruguay and present a key to the four known species of the genus. The male and pupa of one of these new species, *C. dycei*, are the first known for the genus. *C. schnacki*, originally known only from Ecuador, also occurs in northern Argentina as we recently discovered a female taken 16 II 1969 by Martinez and Woodruff from Salta Province, Dto. San Martin, Rio Carapari, 8 km S. Pocitos in the collection of the Museo de La Plata, Argentina.

As a result of some peculiarities found in one of the new species (*C. dycei*), the generic diagnosis for *Clastrieromyia* as originally proposed by Spinelli and Grogan should be amended as follows: Wing with costa extending 0.87–0.98 in females. Antenna 0.9–1.3 times longer than breadth of head. Eversible glands of female abdomen usually with sclerotized gland rods (gland rods unsclerotized in *C. dycei* n. sp.).

The types of the new species are deposited in the collection of the Museo de La Plata, La Plata, Argentina (MLP) and the National Museum of Natural History (USNM), in Washington, D.C. Some paratypes will be deposited in the Australian National Insect Collection (ANIC), Canberra, Australia.

For an explanation of general ceratopogonid terminology see Downes and Wirth (1981); for special terms dealing with genera in the tribe Palpomyiini, see Grogan and Wirth (1979, 1981).

KEY TO SPECIES FOR FEMALE *CLASTRIEROMYIA*

1. Fore femur without ventral spines; costal ratio 0.98
..... *schnacki* Spinelli and Grogan
- Fore femur with 5–10 ventral spines; costal ratio 0.96 or less 2

2. Legs banded, proximal $\frac{2}{3}$ – $\frac{3}{4}$ of fore and mid tibiae and mid femur light brown, remainder of femora and tibiae dark brown *uruguayensis* n. sp.
- Legs unbanded, femora dark brown, tibiae dark or lighter brown but uniformly so 3
3. Small species, wing length 1.55–1.67 mm; narrow interocular space, 2.5–3.5 ommatidial facets wide; antennal ratio 1.29–1.46; gland rods present; costal ratio 0.92–0.96 *kremeri* Spinelli and Grogan
- Large species, wing length 1.97–2.20 mm; broad interocular space, 6–7 ommatidial facets wide; antennal ratio 0.66–0.82; gland rods absent; costal ratio 0.87–0.88 *dycei* n. sp.

***Clastrieromyia dycei*, NEW SPECIES**

Fig. 1

Diagnosis.—A large species (wing length 1.97–2.20 mm) of *Clastrieromyia* distinguished from all other species in the genus by the absence of sclerotized abdominal gland rods (see key for a comparison with other species in the genus).

Female.—Wing length 2.08 (1.97–2.20, $n = 4$) mm; breadth 0.80 (0.77–0.82, $n = 4$) mm.

Head: Dark brown. Eyes bare, broadly separated (Fig. 1a) for a distance equal to the diameter of 7 ommatidial facets. Antennal flagellum (Fig. 1b) short, $0.9 \times$ the breadth of head, uniformly dark brown; lengths of flagellomeres in proportion of 16-9-9-9-9-9-9-12-13-13-13-14; antennal ratio 0.74 (0.66–0.82, $n = 3$). Palpus very short (Fig. 1c), pale brown; lengths of segments in proportion of 8-12-8-8-14; palpal ratio 1.70 (1.50–2.15, $n = 4$); 3rd segment with a few scattered mesoapical sensilla; 5th segment with 4–5 terminal setae. Mandible with 8–12 teeth.

Thorax: Dark brown; scutum without anterior spine or tubercle; scutellum yellowish. Legs slender; femora dark brown, tibiae slightly paler; tarsi whitish except 5th tarsomeres dark brown; fore femur armed with 6–8 ventral spines; ventral palisade setae absent on foretarsus, in one row on tarsomere 1 of mid leg, in two rows on tarsomeres 1 and 2 of hind leg; a pair of strong ventral spines at apices of tarsomeres 1–3 on mid leg, smaller and paler on fore and hind legs; hind tibial comb with 7 spines; hind tarsal ratio 2.30 ($n = 4$); 4th tarsomeres subcylindrical; 5th tarsomeres unarmed, claws equal without internal basal tooth, longest on hind leg. Wing (Fig. 1d) whitish hyaline, anterior veins pale yellow, the others nearly imperceptible; venation as figured, anal lobe well developed, cell R_5 with intercalary vein; costal ratio 0.88 (0.87–0.89, $n = 4$). Halter pale brown.

Abdomen: Yellowish brown, tapering distally; gland rods absent. Genitalia nearly identical to *C. kremeri* as described and illustrated by Spinelli and Grogan (1985), and except for spermathecae are not illustrated or described here. Two unequal oval spermathecae, with short necks and minute hyaline perforations, measuring 0.069 mm by 0.057 mm and 0.057 mm by 0.049 mm including necks; a small vestigial 3rd spermatheca present.

Male.—Wing length 1.40 mm; breadth 0.51 mm. Similar to female with the following notable differences. Antennal flagellum (Fig. 1e) with lengths of flagellomeres in proportion of 20-10-10-9-9-10-10-10-10-11-17-13-19; plume very reduced. Palpus with lengths of segments in proportion of 4-7-6-7-8. Wing (Fig. 1f) with membrane slightly infuscated; costal ratio 0.82. Genitalia as in Fig. 1g:

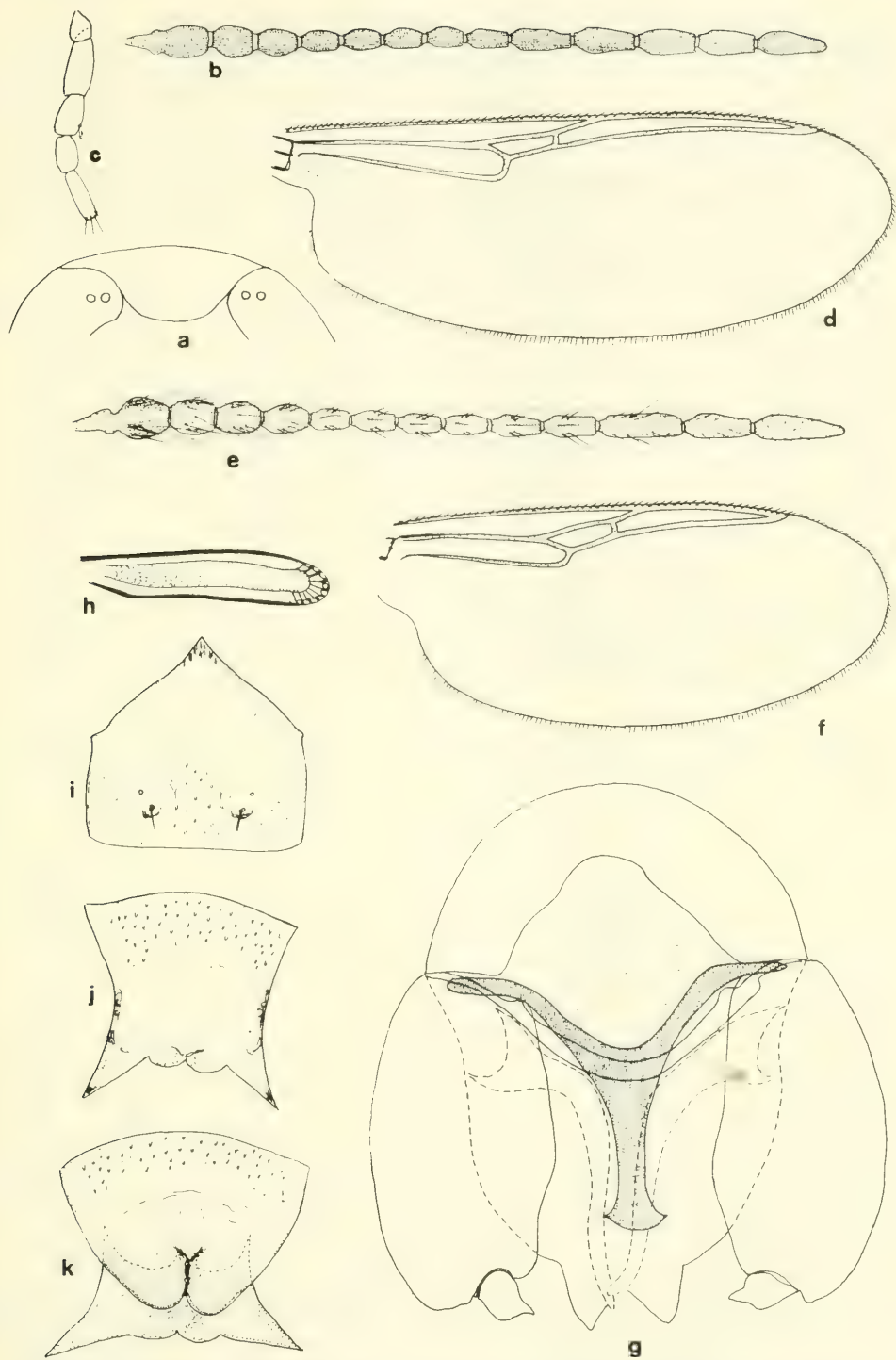


Fig. 1. *Clastrieromyia dycei*, a-d, female; e-g, male; h-k, pupa. a, Eye separation. b, e, Antennal flagella. c, Palpus. d, f, Wing. g, Genitalia. h, Respiratory horn. i, Female operculum. j, Female terminal segment. k, Male terminal segment.

sternite 9 short with a deep caudomedian excavation, caudal membrane spiculate; tergite 9 rounded distally, extending nearly to apex of gonocoxites; cercus short, extending just beyond apex of gonocoxite. Gonocoxite stout, twice as long as broad; gonostylus pointed, very reduced in length. Aedeagus heavily sclerotized, triangular; basal arch extending $\frac{1}{3}$ of total length of aedeagus; basal arm bent at nearly 90° distally; distal portion narrow with broader crescent-shaped tip. Parameres divided, heavily sclerotized; basal arms broad and bifurcate; distal portion slender, each portion produced beyond aedeagus, and extending to near the apex of gonocoxites where their tips cross each other.

Pupa.—Brownish. Length of female 3.5 mm; length of male 3.0 mm. Respiratory horn (Fig. 1h) short, about $\frac{1}{15}$ of total pupal length; 4 times longer than broad; surface bare; apex with 9–11 spiracles. Female operculum (Fig. 1i) as long as broad; anterior margin tapering to a pointed tip, posterior margin nearly straight; surface smooth with a few small tubercles medial to and posterior of *a. m.* tubercles. 2 *a. m.* tubercles, the posterior one bearing a single seta. Female terminal segment (Fig. 1j) with small pointed tubercles only on anterior margin; margins slightly wrinkled, tips heavily sclerotized. Male terminal segment (Fig. 1k) similar to that of female; ventral genital processes short, as figured.

Distribution.—Uruguay (Department of Tacuarembó).

Types.—Holotype ♀, allotype ♂ (USNM), 3 ♀, 3 ♂ paratypes all with associated pupal exuviae, Uruguay, Tacuarembó, Estancia Ipoa, 29-IX-1980, A. Dyce.

Discussion.—We are pleased to name this species in honor of Dr. Alan L. Dyce, of the C.S.I.R.O., McMaster Laboratory, Glebe, Australia, who collected the type-series.

The type-series were reared from pupae that were collected from a cattle-trodden bog adjacent to an excavated watering hole, the soil of which was sandy and sunlit.

Clastrieromyia uruguayensis, NEW SPECIES

Fig. 2

Diagnosis.—Distinguished from all other species in the genus by its banded legs with spinose fore femora, and by the very lightly sclerotized gland rods (see key for a comparison with other species in the genus).

Female.—Wing length 1.86 (1.70–1.94, $n = 3$) mm; breadth 0.75 (0.67–0.79, $n = 3$) mm.

Head: Dark brown. Eyes bare, separated (Fig. 2a) by a distance equal to the diameter of 6 ommatidial facets (0.12 mm). Antennal flagellum (Fig. 2b) short, dark brown; lengths of flagellomeres in proportion of 32-19-19-19-20-19-19-18-25-29-29-25-32; antennal ratio 0.87 (0.83–0.94, $n = 4$). Palpus short (Fig. 2c), pale brown; lengths of segments in proportion of 12-28-24-20-25; palpal ratio 1.93 (1.83–2.18, $n = 5$); 3rd segment with scattered mesoventral sensilla. Mandible with 8–11 coarse teeth.

Thorax: Dark brown. Scutum without anterior spine or tubercle; humeral areas pale brown, 2 pale brown spots on the prescutellar area; scutellum yellowish. Legs (Fig. 2d) dark brown except proximal $\frac{2}{3}$ of mid femur, proximal $\frac{3}{4}$ of fore and mid tibia lighter brown; tarsomeres 1–3 of fore and mid legs and tarsomeres 1 and 2 on hind leg whitish; fore femur armed with 5–8 ventral spines; mid tibia with a pair of strong ventral spines at apex; ventral palisade setae absent on foretarsus, in one row on tarsomere 1 of mid leg, in two rows on tarsomeres 1

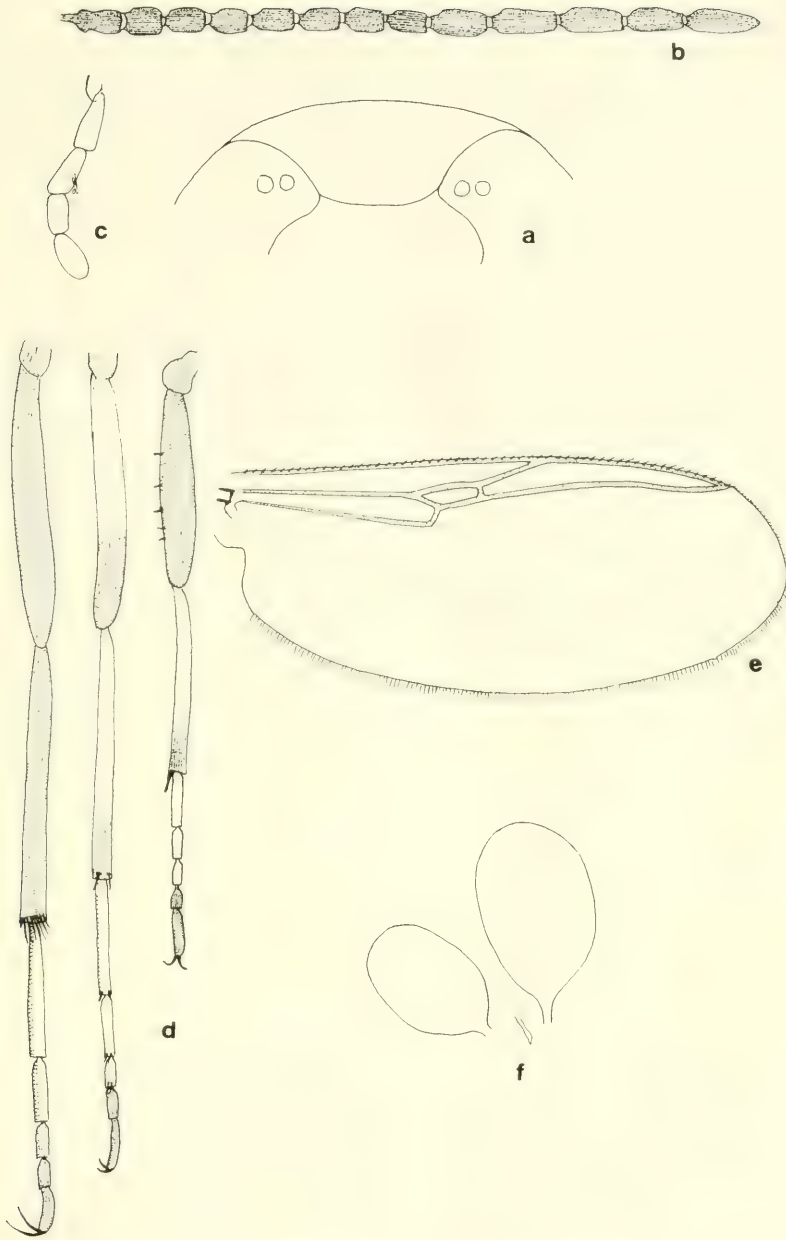


Fig. 2. *Clastrieromyia uruguayensis*, female. a, Eye separation. b, Antennal flagellum. c, Palpus. d, Legs. e, Wing. f, Spermathecae.

and 2 of hind leg; a pair of strong ventral spines at apices of tarsomeres 1–3 on mid leg, smaller and paler on fore and hind legs; hind tibial comb with 7 ($n = 5$) spines; hind tarsal ratio 2.28 (2.10–2.52, $n = 5$); 4th tarsomeres subcylindrical, 5th tarsomeres unarmed, claws equal without internal basal tooth, longest on hind leg. Wing (Fig. 2e) whitish hyaline, anterior veins pale yellow, the others nearly

imperceptible; venation as figured, anal lobe well developed, cell R_5 with intercalary vein; costal ratio 0.89 (0.88–0.90, $n = 3$). Halter white.

Abdomen: Whitish, tapering abruptly distally, with reddish spots on pleurae of segments 2–6. Genitalia nearly identical to *C. kremeri* as described by Spinelli and Grogan (1985) and except for spermathecae are not illustrated or described here. Two unequal oval spermathecae (Fig. 2f) with short necks and minute hyaline perforations, measuring 0.080 mm by 0.053 mm and 0.058 mm by 0.043 mm including necks; a small vestigial 3rd spermatheca present.

Male.—Unknown.

Distribution.—Uruguay (Departments of Atigas and Salto).

Types.—Holotype ♀, Uruguay, Artigas, Colonia San Gregorio ("arrocera de Conti"), 12-II-1985, G. R. Spinelli, light trap (MLP). Paratypes, 4 ♀, as follows: same data as holotype, 1 ♀; same data except 18-III-1985, 2 ♀; Uruguay, Salto, El Espinillar, 14-II-1985, G. R. Spinelli, 1 ♀, light trap.

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EXPLORATION FOR AND IMPORTATION OF NATURAL ENEMIES
OF THE GYPSY MOTH, *LYMANTRIA DISPAR* (L.)
(LEPIDOPTERA: LYMANTRIIDAE), IN NORTH AMERICA:
AN UPDATE

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Abstract.—A compendium report of explorations, importations, and releases of exotic natural enemies of the gypsy moth in the United States, published in 1981, is updated. Changes in scientific nomenclature of the natural enemies, and information on explorations and importations, that have occurred from 1978–1985, and literature published during that period, are reported. A complete record of importations from 1963–1985 is provided. One pupal parasite, *Coccygomimus disparis* (Viereck) (Ichneumonidae), is established in the United States as a result of these importations. A second parasite, *Meteorus pulchricornus* (Wesmael) (Braconidae), has been recovered and may be considered provisionally established. Data on importations of gypsy moth natural enemies into Canada, which began in 1976, are also summarized.

There exist excellent accounts and records of the importation and release of foreign natural enemies of the gypsy moth, *Lymantria dispar* (L.) (Lep.: Lymantriidae), in the United States since foreign explorations began in 1905 through 1960. The most comprehensive of these records are by Howard and Fiske (1911), Burgess and Crossman (1929), Dowden (1962), and the more recent summary by Clausen (1978).

In 1981, a compendium report (Doane and McManus, 1981) was published by the U.S. Department of Agriculture presenting the results of extensive cooperative research on the gypsy moth and on various measures for its control that had been conducted primarily under specially authorized funds. (The Expanded Research, Development and Application Program was funded through the U.S. Department of Agriculture (USDA) from 1975–1978; an earlier accelerated gypsy moth program was funded by the USDA from 1971–1974 (McManus and McIntyre, 1981).) Included in the 1981 book was a section on parasites (Chapter 6.1), various

portions of which were written by a number of cooperating scientists, and a major portion of which represented a description of the gypsy moth natural enemy exploration, importation and release activities that had been conducted from 1961 through 1977.

Since 1977, which was the cut-off date for manuscripts submitted for the compendium report finally published in 1981, there have been 1) a number of important taxonomic papers published which permit the up-dating of the scientific nomenclature used for the natural enemies in the 1981 publication, and 2) additional explorations, importations, releases, and recoveries of exotic natural enemies of the gypsy moth. The purposes of this paper are 1) to up-date the record of foreign species of gypsy moth natural enemies shipped to the United States, presented in Table 6.1-1 of the 1981 publication, 2) to provide corrected and new scientific names for the natural enemies as required, 3) to extend the record of importations from 1978–1985, and 4) to correct several errors in the original table. A brief account will also be given of the foreign exploration activities that have been conducted from 1978 through 1985, and of the publications relating to gypsy moth foreign explorations that have appeared since 1977 and thus did not appear in the 1981 publication.

Release information as such is not a subject for discussion here. We record shipments only to the point of "Shipped from quarantine"; field releases may not have ultimately resulted. A summary record of the releases of gypsy moth natural enemies in the United States, 1963–1977, was published by Doane and McManus (1981). In addition, Dr. Richard J. Dysart, ARS, Beneficial Insects Research Laboratory, Newark, Delaware, is completing a more detailed computerized record of the releases of gypsy moth parasites and predators from 1962 through 1985. These records will be published, and will complete the accounting of the most recent period of foreign exploration, importation and release of natural enemies of the gypsy moth in the United States.

TAXONOMY AND NOMENCLATURE

Authors preparing papers for the parasite section of Doane and McManus (1981) benefited from having at hand the recent taxonomic treatise on the tachinid (Diptera) parasites of the gypsy moth by Sabrosky and Reardon (1976). The nomenclature for that group of parasites is thus fairly up-to-date. Since then, similar treatises have appeared concerning the braconid and ichneumonid (Hymenoptera) parasites of the gypsy moth by Marsh (1979) and Gupta (1983), respectively. Other taxonomic publications that pertain to the species listed and nomenclature used in Doane and McManus (1981) are the Catalog of Hymenoptera of North America by Krombein et al. (1979), the revision of Oriental Pori-zontini (Ichneumonidae) by Gupta and Maheshwary (1977), and the revision of the braconid subfamily Microgastrinae by Mason (1981).

These sources, and some unpublished manuscripts and identifications received after 1977, were utilized in the preparation of Table 1, presented here, which is a revision and extension of Table 6.1-1 of Coulson (1981). P. M. Marsh, USDA, ARS, Systematic Entomology Laboratory, Beltsville, Maryland, has very kindly provided the correct generic placement for those species formerly in the genus *Apanteles* (Braconidae) that were not listed by Mason (1981).

FOREIGN EXPLORATION AND IMPORTATION

A number of papers were published after 1977 presenting more details of the explorations discussed in Doane and McManus (1981): in Morocco (Hérard, 1979; Hérard and Fraval, 1980); Poland (Drea and Fuester, 1979); Iran (Hérard et al., 1979); Austria and Germany (Fuester et al., 1983); Japan (Schaefer et al., 1979; Schaefer and Shima, 1981; and Schaefer and Ikebe, 1982); and India (Dharma-dhikari et al., 1985). A manuscript concerning explorations in France is in preparation by RWF and others.

Other than one additional exploration trip, to Romania in 1978 specifically for collection of pupal parasites (see Hedlund and Mihalache, 1980), the gypsy moth activities of the Agricultural Research Service (ARS) European Parasite Laboratory (EPL) in Europe were confined to "mail order" type collections in 1978–1985. (See Drea, 1978, for a summary of EPL's earlier work.) Such collections were made in France, Austria, and by cooperative arrangements, in Italy (Sardinia). The natural enemy species that were shipped to the United States as a result of those collections are reported in Table 1.

The ARS Asian Parasite Laboratory in Japan continued its field studies in Japan and Korea during 1978 to 1981, and the natural enemies shipped to the U.S. are shown in Table 1. In February 1982, the Laboratory was moved to Seoul, South Korea, and during that year surveys for natural enemies of the gypsy moth were carried out but no shipments were made to the U.S. Shipments of natural enemies from South Korea were made in 1983–1985 and are reported in Table 1.

In 1984, Richard S. Soper (ARS, Plant Protection Research, Ithaca, New York) collected an entomogenous fungus in Japan, where it was causing considerable mortality of gypsy moth larvae on the west coast of Honshu, and brought isolates back for study and experimental release of the fungus in the United States (see Table 1).

In 1981, as a direct result of the publication (Marsh, 1979) of descriptions of new species of braconid parasites of the Indian gypsy moth, *Lymantria obfuscata* Walker, discovered during earlier explorations in India by the Commonwealth Institute of Biological Control (CIBC) as reported by R. C. Reardon and Coulson (in Doane and McManus, 1981), RWF entered into another contract with the Indian Station of the CIBC for collection of specific parasite species. The natural enemies collected in India and shipped to the U.S. by Dr. G. Ramaseshiah of CIBC in 1981, and again under contract in 1982, are shown in Table 1. Some of these parasites, especially the braconid *Glyptapanteles flavicoxis* and the ichneumonid *Hyposoter lymantriae*, appear quite promising, particularly for use in parasite augmentation programs against the gypsy moth. Several of the species were placed in culture from which releases continued through 1985.

Also in 1981, a team of forest entomologists from USDA's Forest Service (USFS) and the Pennsylvania Bureau of Forestry traveled to the Soviet Union, and they were able to collect gypsy moth natural enemies for shipment to the U.S. (Ticehurst, 1982; Coulson, 1982). The species received from these collections in the Ukraine are listed in Table 1.

Beginning in 1979, a series of visits to the People's Republic of China by U.S. biological control specialists was carried out under a U.S./PRC Agreement on Cooperation in Science and Technology (see Coulson et al., 1982; McFadden et

Table 1. Foreign species of gypsy moth natural enemies shipped to the United States, 1963-1985¹

Taxonomic Classification and Genus and Species ²	Origin of Collections and Years of Shipment ³				Shipped from Quarantine ⁴	
	1963-71	1972-74	1975-77	1978-85	1963-77	1978-85
Hymenoptera:						
Braconidae:						
" <i>Apanteles</i> " spp. indet. (See also <i>Glyptapanteles flavicoxis</i> and <i>G. indiensis</i>)	S ^{9,5} Y ^{9,6} In ^{9?}	In*	In*	In(81-82)	+	-
<i>Cotesia melanoscela</i> (Ratzeburg) (= <i>Apanteles melanoscelus</i> (Ratz.))	Y, In ⁷	A, F, G, M, Y	A, F, In, Ir, J, P	Sa(80), J, U(81), K(83-85) ²⁶	+	+
(= <i>A. solitarius</i> (Ratzeburg))						
(= <i>A. ?ruidus</i> Wilkinson)						
(= " <i>A. spp.</i> " indet., in part)						
<i>C. schaeferi</i> (Marsh) (= <i>Apanteles schaeferi</i> Marsh) (= " <i>A. n.sp.</i> ")			J	J(78) K(83-85)	+	+
<i>Dolichogenidea lacteicolor</i> (Viereck) (= <i>Apanteles lacteicolor</i> Viereck)			F†, In, Ir	In(81-82)	+	-
<i>Glyptapanteles flavicoxis</i> (Marsh) (= <i>Apanteles flavicoxis</i> Marsh) (= " <i>A. spp.</i> " indet. from India (Kulu), in part)	In ^{9?}	In*	In*	In(81-82)	?	+
(= " <i>A. sp. nr. conspersae</i> ")						
<i>G. indiensis</i> (Marsh) (= <i>Apanteles indiensis</i> Marsh) (= " <i>A. spp.</i> " indet. from India (Srinagar), in part)	In ^{9?}	In*	In*	In(81-82)	?	+
(= <i>A. liparidis</i> from India, at least in part)						
<i>G. liparidis</i> (Bouché) (= <i>Apanteles liparidis</i> (Bouché)) (= " <i>A. spp.</i> " from Yugoslavia, in part) (See also <i>G. indiensis</i>)	S ^{9,5} Y, In ^{9?}	A, F, G, J, Y	A, F, In?, Ir, J, M, P, Y	F(81,85), In(81), Ch*, K*(83,85)	+	+

Table 1. Continued.

Taxonomic Classification and Genus and Species ²	Origin of Collections and Years of Shipment ¹				Shipped from Quarantine ⁴	
	1963-71	1972-74	1975-77	1978-85	1963-77	1978-85
<i>G. porlhetriæ</i> (Muesebeck) (= <i>Apanteles porlhetriæ</i> Mues.)	S	A, F, G, M	A, C, F, M, P	Sa(80), U(81)	+	-
<i>Meteorus pulchricornis</i> (Wesmael) (= <i>M. japonicus</i> Ashmead) (= <i>M. spp.</i> indet.)		A, F, M, Y	A, Ir, J*, M, P	A, F, U*(81), K(84)	+	+
† <i>M. versicolor</i> (Wesmael)			F			
<i>Protapanteles lymantriæ</i> (Marsh) (= <i>Apanteles lymantriæ</i> Marsh)			J(79)		+	-
<i>Rogas indiscretus</i> Reardon (= <i>Rogas</i> sp.)	In		In		+	
<i>R. lymantriæ</i> Watanabe			J	J(78)	+	-
Ichneumonidae:						
<i>Casinaria arjuna</i>				K(83-84)		+
Mareshwary & Gupta						
<i>Casinaria elegantula</i>				In(82)		-
Mareshwary & Gupta						
<i>C. nigripes</i> (Gravenhorst) (= <i>C. spp.</i> indet.)		F	A*	F(84)	+	-
<i>C. tenuiventris</i> (Gravenhorst)						
<i>Coccysgomimus disparis</i> (Viereck) (= <i>C. sp.</i> indet. from India, in part) (= <i>Pimpla</i> sp.)	In*	A, F, G In	J	A, F(81) K(84)	+	+
<i>C. instigator</i> (F.)		M, Y M	Ir, P	R(78)	+	+
<i>C. moraguesi</i> (Schmiedeknecht) (= <i>C. turionellæ moraguesi</i> (Schm.)) (= <i>Pimpla</i> sp.)					+	

Table 1. Continued.

Taxonomic Classification and Genus and Species ²	Origin of Collections and Years of Shipment ³					Shipped from Quarantine ⁴	
	1963-71	In*	In	1972-74	1975-77	1978-85	1963-77 1978-85
<i>C. turionellae</i> (L.) (= <i>C. t. turionellae</i> (L.)) (= <i>C. sp. indet. from India, in part</i>) (= <i>Pimpla</i> sp.)			In			R(78)	+
<i>C. spp. indet.</i>			C		M*		+
<i>Ephialtes compuncator compuncator</i> (L.)						R(78)	+
† <i>Gregopimpla himalayensis</i> (Cameron) ⁸						J(78)	-
<i>Hyposoter lymantriae</i> Cushman						In(82)	+
<i>H. tricoloripes</i> (Viereck)			A, F, G		A, F, P	F(80)	+
<i>Ichneumonid</i> spp. indet. ⁹		Y	M		M*		+
<i>Lymantrichneumon disparis</i> (Poda)					Ir		-
† <i>Meloboris</i> (sens. lat.) sp.					P		+
<i>Phobocampe lymantriae</i> Gupta (= <i>P. spp. indet., in part</i>)		Y?	A*, F*, G?*, Y?*		P	K(84-85)	+
<i>P. uncinata</i> (Gravenhorst) (= <i>P. disparis</i> (Viereck)) (= <i>P. spp. indet., in part</i>)		Y?	A, F, G		A, F, Ir*, Y	J(78), F*(80,85), J*, U*(81)	+
<i>Theronia atalantiae atalantiae</i> (Poda)							+
† <i>Tranosema rostrale</i> (Brischke) (= " <i>T. arenicola</i> ")					P	R(78)	+
<i>Vulgichneumon</i> sp. ¹⁰ (= <i>Melanichneumon</i> sp.)			M		M*		+
Eulophidae:							
† <i>Trichoplectrus laeviscuta</i> (Thompson) (= <i>Euplectromorpha "laeviscuta</i> (Thompson)")			F				-

Table 1. Continued.

Taxonomic Classification and Genus and Species ²	Origin of Collections and Years of Shipment ³				Shipped from Quarantine ⁴	
	1963-71	1972-74	1975-77	1978-85	1963-77	1978-85
Encyrtidae:						
<i>Ooencyrtus kuvanae</i> (Howard)		F, M*			+	
Eupelmidae:						
<i>Anastatus disparis</i> Ruschka ¹¹ (= <i>A. japonicus</i> Ashmead) (= <i>A. bifasciatus</i> (Fons.)) (= <i>A. sp.</i> "blue" ex France) <i>A. ?kashmirensis</i> Mathur <i>A. spp.</i> indet. ¹³		F	A, F	J*(78-79), Ch*(81)	+	+ ¹²
Torymidae:						
<i>Monodontomerus aereus</i> Walker	In		In Ir*		+	+
Chalcididae:						
<i>Brachymeria intermedia</i> (Nees) <i>B. lasus</i> (Walker) ¹⁴ (= <i>B. "euplocae"</i> of authors) <i>B. spp.</i> indet. ¹⁵	S, In	C, F, M, Y	In*, M* In, J In*	R(78) K(78,84)†	+	+ +
Scelionidae:						
<i>Gryon sp.</i> indet. ¹⁶ <i>Hadronotus sp.</i> indet. <i>Telenomus spp.</i> indet.			M F M ¹⁶		- - -	
Family indet.						
"Hymenoptera sp. indet." ¹⁹	Y				+	

Table 1. Continued.

Taxonomic Classification and Genus and Species ²	Origin of Collections and Years of Shipment ³			Shipped from Quarantine ⁴	
	1963-71	1972-74	1975-77	1978-85	1963-77 1978-85
Diptera:					
Sarcophagidae:					
<i>Agria affinis</i> (Fallén)		F, Y		J(79)	+
<i>Robineauella pseudoscopia</i> (Kramer) ¹⁷ (= " <i>Sarcophaga</i> sp.")					-
Tachinidae:					
<i>Blepharipa pratensis</i> (Meigen) (= <i>B. scutellata</i> (R.-D.))		A, C, F, G, Y	A*, F*, P*		+
<i>B. schineri</i> (Mesnil)			J†	J(79) Ch(83), K(85)	+
† <i>B. "sericariae</i> (Rondani)"			J		-
<i>B. sp. indet.</i> ¹⁸			J	J(78-79)	-
<i>Blondelia nigripes</i> (Fallén)		A	P	U(81)	-
<i>Carcelia separata</i> (Rondani) (= <i>C. "excisa"</i> of authors)		A, F	A, Ir, M, P	F(81)	-
<i>C. sp. indet.</i> ¹⁹		Y			+
<i>Ceranthia samarensis</i> (Villeneuve) (= <i>Siphona samarensis</i> (Vill.))		A			-
<i>Compsitura concinnata</i> (Meigen)		A, F, Y	Ir*, J*, M*, P*	U(81)	+
<i>Euphorocera</i> sp. indet.		F			+
<i>Eusisyropa</i> sp. indet.		F			+
<i>Exorista japonica</i> (Townsend) (= " <i>Parasetigena</i> sp." in part)			J	J(78-79)	-
<i>E. larvarum</i> (L.)	Y		Ir	R(78)	+
<i>E. rossica</i> Mesnil	In	In			+
<i>E. segregata</i> (Rondani) (= <i>Tricholyga segregata</i> (Rond.))	S				+

Table 1. Continued.

Taxonomic Classification and Genus and Species ²	Origin of Collections and Years of Shipment ¹				Shipped from Quarantine ⁴	
	1963-71	1972-74	1975-77	1978-85	1963-77	1978-85
<i>†E. sorbillans</i> (Wiedemann)			K		-	
<i>Palexorista disparis</i> Sabrosky ²⁰ (= "Drino discreta" of authors) (= <i>Palexorista</i> sp.)	In	In			+	
<i>P. inconspicua</i> (Meigen) (= "Drino inconspicuides" of authors)	In	F			+	
<i>P. spp.</i> indet. (2 spp.?)		F, Y	M*		+	
<i>Parasetigena silvestris</i> (Robineau-Desvoidy) (= "P. agilis" of authors)		A, F, G, Y	A*, F*, J*, P*	J(79), Ch(83) K(85)	+	+
<i>P. spp.</i> indet. (2 spp.?) ²¹			J†, K	J(78-79)	-	-
<i>†Phorocera assimilis</i> (Fallén)			J		-	
"P. sp." indet.		Y			+	
"Sturmia sp." indet.	Y				-	
Tachinid spp. indet. ²²	Y	Y*, M*	Ir*, J*, K*, Y*	J(78-79), U(81)	+	-
Heteroptera:						
Pentatomidae:						
<i>Dinorhynchus dybowskyi</i> Jakovlev			J	J(78-81,85)	-	+
Pentatomid sp. indet. (nymph)			Ir		-	
Coleoptera:						
Carabidae:						
<i>Calosoma maximoviczi</i> (Morawitz)				J(78)		-
<i>C. sycophanta</i> (L.)		A, Y	A*, Ir*, M*		+	
Silphidae:						
<i>Xylodrepa sexcarinata</i> Motschulsky				J(79)		-

Table 1. Continued.

Taxonomic Classification and Genus and Species ²	Origin of Collections and Years of Shipment ³				Shipped from Quarantine ⁴	
	1963-71	1972-74	1975-77	1978-85	1963-77	1978-85
Dermestidae:						
<i>Anthrenus verbasci</i> (L.)	M				-	
<i>Trogoderma versicolor</i> (Creutzer) ²³	M				- ²³	
Trogositidae:						
<i>Tenebroides maroccanus</i> Reitter	M				-	
Tenebrionidae:						
<i>Akis bacarozzo</i> (Schrank)		M			-	
Nematoda:						
Mermithidae:						
<i>Hexameris</i> spp. (4 spp.?) ²⁴	A, G		A, J, U	J(79,82), F(80), In(82)	+	+
Pathogens: viral, fungal	A, G		A, In, Ir, J, P	J(78-79, 84), R(78) Ch(80-83), In(82), K(84) ²⁵	+	+

¹ This is a nomenclatural up-dating of Table 6.1-1 of Doane and McManus 1981, and includes an additional 7 years of shipment data.

² A dagger sign (†) in this column (or in the source column) indicates that that species (or that species from that source) was collected from hosts other than gypsy moths (*Lymantria dispar* (L.) and Oriental subspecies, and *L. obfuscata* (Walker) in India) for trial on gypsy moth in the U.S.; *Dolichogenidea lacteicolor* and *Meteorus versicolor* from France were recovered from the brown-tail moth, *Euproctis chrysorrhoea* (L.); *Gregopimpla himalayensis* from Japan were recovered from *Orgyia recens approximans* Butler; *Meloboris* sp. and *Tranosema rostrale* from Poland were recovered from the rusty tussock moth, *Orgyia antiqua* (L.); *Brachymeria lasus* from Korea were recovered from the fall webworm, *Hyphantria cunea* (Drury); the *Blepharipa "sericariae"* and the 1976 shipment of *Parasetigena* sp. from Japan, and *Exorista sorbillans* from Korea, were recovered from the silkworm, *Bombyx mori* (L.). *Blepharipa schineri* and *Phorocera assimilis*, and some of *B.* sp. indet. and *Parasetigena silvestris*, from Japan in 1977, were collected as adults from a gypsy moth infestation, and thus actual hosts are unknown.

³ A = Austria; C = Corsica; Ch = People's Republic of China; F = France; G = Germany; In = India; Ir = Iran; J = Japan; K = Korea; M = Morocco; P = Poland; R = Romania; S = Spain; Sa = Sardinia; U = USSR; Y = Yugoslavia.

⁴ A plus sign (+) in this column indicates shipments of the species were made from quarantine (ARS Beneficial Insects Research Laboratory (BIRL), Newark, Delaware). An asterisk (*) in the Origin column indicates material from that source was not included among material shipped from quarantine.

⁵ "Apanteles spp." shipped from Spain in 1964-65 and 1968-69 were first shipped as "*A. vitripennis*," and were later found to include primarily *Glyptapanteles porthetriae*, but possibly also included *G. liparidis* and other species.

- ⁶ "*Apanteles* spp." shipped from Yugoslavia in 1970 included primarily *Glyptapanteles liparidis*, with some *Cotesia melanoscela* and possibly other species including *C. ocnertia* (Ivanova).
- ⁷ "*Apanteles* spp." shipped from India in 1970–71 probably included *Glyptapanteles flavicoxis*, *G. indiensis*, *G. liparidis*, and *Cotesia melanoscela*, and possibly other species.
- ⁸ Gupta (1983) treats *Gregopimpla* as a subgenus of *Iseropus*; these are considered separate genera by R. W. Carlson in Krombein et al. (1979).
- ⁹ In 1970, one shipment of 8 adults of "ichneumonid sp.," and one shipment of a single adult "Hymenoptera sp.," all of Yugoslavian origin, were shipped from quarantine to the New Jersey Department of Agriculture (NJDA), Trenton. In 1974, a shipment of a single adult "ichneumonid sp." from Morocco was sent to NJDA from quarantine. In 1975, two adult "ichneumonid sp." emerged and died in quarantine from Moroccan material. According to R. J. Dysart and L. R. Erle (BIRL, ARS; personal communication, 1982), the Yugoslavian specimens were probably *Phobocampe* sp., and the Moroccan specimens *Vulgichneumon* (= *Melanichneumon*) sp. However, no specimens exist to confirm this. There was no culture or release of any of this material.
- ¹⁰ Gupta (1983) treats *Vulgichneumon* as a subgenus of *Melanichneumon*; these are considered separate genera by R. W. Carlson in Krombein et al. (1979).
- ¹¹ Determination of the 1978–81 specimens are by E. E. Grissell, Systematic Entomology Laboratory (SEL), ARS, Washington, D.C.
- ¹² Shipment made in 1979 from quarantine was from a laboratory culture originating from 1976 Austrian collections.
- ¹³ The "*Anastatus* spp." from India in 1966–67 may have included *A. ?kashmirensis* and other species.
- ¹⁴ Correction of misidentification by E. E. Grissell, SEL, ARS. The Indian population was uniparental, the Japanese population biparental. No live material was received from Korea in 1978.
- ¹⁵ The 1972 and 1976 material from India was probably *B. intermedia* but may have included *B. lasus*; the few adults that emerged from the 1976 material were *B. intermedia*.
- ¹⁶ Shipments of "*Telenomus* spp." from Morocco in 1975–76 included 1–2 species of *Telenomus* and a species of *Gryon*; the latter may possibly be a parasite of pentatomid eggs rather than of gypsy moth eggs.
- ¹⁷ Determination by R. J. Gagné, SEL, ARS.
- ¹⁸ Some of the 1977 material was collected as adults; see footnote 2. The unemerged and/or undetermined Japanese specimens from 1976–79 collections were probably *B. schineri*; some adults emerged from the 1979 material and were identified as *B. schineri* by D. D. Wilder, SEL, ARS.
- ¹⁹ This 1973 shipment from Yugoslavia was apparently never identified and may have been *C. separata*.
- ²⁰ Shipments of this species, as "*Drino discreta*," may have included some *P. solennis* (Walker) (see Sabrosky and Reardon, 1976).
- ²¹ The *Parasetigena* sp. from *Bombix mori* was from Japan in 1976 (not from Korea as given in Table 6.1-1 of Coulson in Doane and McManus (1981). The *P.* sp. from Korea in 1977 was from *Lynantria dispar*, and is probably a new species, according to C. W. Sabrosky, SEL, ARS, *in litt.*, 1978.
- ²² Many shipments of tachinid puparia were received from which no adults emerged and thus no identifications were made; these may represent species listed above.
- ²³ Table 6.1-1 of Coulson in Doane and McManus (1981) is in error; no live specimens of this species were removed from quarantine.
- ²⁴ Taxonomic study of specimens of the 1974–1977 European and Japanese gypsy moth nematodes were conducted by H. Kaiser (University of Graz, Austria), and W. R. Nickle (ARS, USDA, Beltsville, MD) in 1978. Four new species of *Hexameris* were described in an as yet unpublished manuscript: one from Austria, one from the USSR, and two from Japan.
- ²⁵ The fungus *Beauveria* was received from Romania (1978) and *Entomophthora* was received from Japan (1978–79) and India (1982), and *E. aulicae* (Reichardt) Humber was collected in Japan by Dr. R. S. Soper (ARS, Ithaca, NY) in 1984; nuclear polyhedrosis virus (NPV) of *L. dispar* was received from Japan (1978), the People's Republic of China (1980–83), and South Korea (1984).
- ²⁶ The Korean *C. melanoscela* is believed to be a different biotype of the species already established in the United States, and is dubbed "halo" because of a distinct silk halo surrounding the cocoon of this strain.

al., 1981). Visiting U.S. scientists brought back samples of gypsy moth virus from China in 1980, 1981 and 1982. The 1980 material was sent to Pennsylvania State University (Coulson et al., 1982: Appendix 23), while the 1981–1982 material was sent to the U.S. Forest Service laboratory at Hamden, Connecticut (Lewis et al., 1984). A shipment of *Anastatus* parasites was also received from China in 1981 for study at the ARS laboratory in Newark, Delaware (Coulson, 1982; Fuester, 1982). The 1982 team of U.S. scientists visiting China, consisting of PWS, W. E. Wallner (USFS, Hamden, Connecticut) and R. M. Weseloh (Connecticut Agricultural Experiment Station, New Haven), was able to conduct a rather extensive survey of the gypsy moth and its natural enemies during their travels (Schaefer et al., 1984a, b). PWS returned to China in 1983, with T. M. O'Dell (USFS, Hamden, Connecticut), for intensive collections in Heilongjiang Province of northeast China. Some live univoltine tachinid parasites were returned to ARS quarantine facilities in Delaware, overwintered, and some F_1 material was released in Delaware in 1985. A paper on the results of the 1983 studies in China is planned. These various shipments of Chinese natural enemies are all noted in Table 1.

Some account of recent work at the ARS Beneficial Insects Research Laboratory at Newark, Delaware, has been given by Fuester (1982, 1985) and Schaefer (1982).

NATURAL ENEMY IMPORTATIONS IN CANADA

To conclude this brief up-date on recent gypsy moth explorations and importations, a few notes on activities in Canada are required. An account of the biological control efforts against the gypsy moth in Canada from 1969 through 1980 was published by Griffiths and Quednau (1984). In view of the spread of the gypsy moth into Canada, Canadian forest entomologists began natural enemy surveys in Canada and have funded some studies on the biological control of the gypsy moth at the European Station of the CIBC since 1974. Apparently the first importation of gypsy moth natural enemies in Canada was the release of the egg parasite, *Ooencyrtus kuvanae*, from the U.S. in Ontario in 1976 (Williamson, 1980; Griffiths and Quednau, 1984). The egg parasite *Anastatus disparis* was imported from Hungary and Romania and released in Quebec in 1979 and in Quebec and Ontario in 1980 (Williamson, 1981a, b; Griffiths and Quednau, 1984). Additional *O. kuvanae* were imported from the U.S. and released in Quebec in 1982, and more *A. disparis* were imported from Europe and released in Ontario and Quebec in 1982 and in New Brunswick, Quebec and Ontario in 1983. A small release of the tachinid parasite *Parasetigena silvestris* from South Tirol, Austria, received from the CIBC, was made at Kaladar, Ontario, in 1984 to supplement the genetic pool of that species. The tachinid *Ceranthia samarensis* was reared from artificial infestations of gypsy moth made by the CIBC in France, in 1984 and 1985. These are being studied by F. W. Quednau, Laurentian Forest Centre, Ste. Foy, Quebec, and V. Nealis, Great Lakes Forestry Centre, Sault Ste. Marie, Ontario. No field releases of this species have been made as yet.

ESTABLISHMENTS

The goal of any natural enemy exploration/importation program is, of course, to establish natural enemies that will be effective in reducing damage caused by the target pest. Establishments resulting from the early gypsy moth natural enemy

importation programs have been reported by a number of authors, including Burgess and Crossman (1929), Dowden (1962), and Clausen (1978). Although several of the newly imported species have been recovered in the field in the year of release, and a few have been recovered in the year following release, there is evidence to date that only two of the natural enemy species newly imported from 1961 to 1985 may have so far become established in the United States. The first is the introduced pupal parasite *Coccygomimus disparis*, which has been sporadically recovered since 1981 and is now believed to be established in Maryland and Pennsylvania (Fuester, 1985) and in New Jersey (R. Chianese, N.J. Department of Agriculture, Trenton, *in litt.*, 1985); a manuscript by PWS and others is in preparation. The second is the larval parasite *Meteorus pulchricornis*, which was recovered from gypsy moth at a single site in Pennsylvania during 1985. No releases of this species had been made in that state since 1977. An earlier single recovery of this polyphagous species had been made in Wisconsin the year following release on a non-gypsy moth lepidopterous host (Shenefelt and Coppel, 1977). No additional recoveries have been made in Wisconsin (H. C. Coppel, University of Wisconsin, Madison, personal communication, 1985).

Hoy (1976) has presented an analysis of the possible reasons for the establishment or non-establishment of some of the parasites imported during the early importation programs, and of some imported early in the more recent program. The scope of this paper does not encompass a record of the release of the natural enemies received, but is only a brief up-dated account of the recent explorations and importations. As noted above, Dr. Dysart is currently completing such a record of releases. No comments can be made here concerning many of the points made by Hoy beyond those made in Doane and McManus, 1981, except that it can be stated that the list of geographical areas noted by Hoy as being inadequately surveyed for new natural enemies of the gypsy moth has been shortened. The apparently strong establishment of *Coccygomimus disparis* as a result of these recent importations is encouraging. Although it is premature to claim establishment of *Meteorus pulchricornis* based on a single recovery, it is also encouraging that this species has managed to survive in nature for eight years following its release in 1977 in Dauphin County, Pennsylvania, the same county in which it was recovered. What, if any, impact these parasites may have on gypsy moth populations, should their own populations build significantly, remains to be seen.

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THE SAWFLY GENUS *NEMATINUS* IN NORTH AMERICA
(HYMENOPTERA: TENTHREDINIDAE)

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Abstract. — Four species of the nematine genus *Nematinus* occur in North America. The genus is transcontinental in Canada to Alaska and northern United States south to California, Utah, and Colorado in the West. Known hosts are *Betula* and *Alnus*. *Nematinus parsebenus*, n. sp., is described from eastern Canada and northeastern United States, and *Pachynematus oronus* Kincaid is a new synonym of *N. pontanioides* (Marlatt). The species are keyed, described, and illustrated.

The small genus *Nematinus*, in the subfamily Nematinae, has received little attention in North America because of the lack of specimens available for study and the apparent obscureness of characters available for species separation. Ross (1951) and Smith (1979) merely listed the four described North American species and noted their type localities. Although I have seen only about 80 specimens, the number is now sufficient to define the North American species. The genus is transcontinental in Canada and northern United States extending south to Colorado, Utah, and California in the West. Known hosts are species of *Betula* and *Alnus*.

About 10 species are found in the Palearctic Region from Europe to Japan where the known hosts are *Betula*, *Alnus*, and *Corylus*. Benson (1958) and Muehle (1977) keyed five species known from Britain and central Europe, respectively. Stein (1926) recorded some life history studies on several European species. Two groups are evident in the Palearctic Region, based on the shape of the female sheath: one with the sheath uniformly broad and truncated at the apex from above and the other with the sheath narrowing and acuminate at the apex from above. Only the latter group is found also in North America.

Females of *Nematinus* are immediately recognized by the large and expanded ninth abdominal segment (Figs. 1, 2), not known elsewhere in the Nematinae except for *Decanematus* Malaise, and the strongly sclerotized and tough ovipositor (Figs. 7-14), which is no doubt an adaptation to oviposition in stems or midveins of the host leaves (Benson, 1958). Well-defined teeth are found on the apical part of the dorsum of the lance and venter of the lancet. Males are scarce; I have seen only about five specimens, but they are more difficult to separate from males of other nematine genera and may be masquerading under other genera in collections.

Nematinus Rohwer

Nematinus Rohwer, 1911: 99. Type species: *Tenthredo abdominalis* Panzer, orig. desig. Ross, 1937: 75, 76, 82-83; Ross, 1951: 37; Smith, 1979: 56.

Description.—Antenna setaceous, $2\frac{1}{2} \times$ head width. Clypeus circularly emarginate at center, with rounded lateral lobes; malar space broad, more than $2 \times$ diameter of front ocellus; left mandible in side view tapering evenly from base to apex, without necklike constriction between base and apical blade. Tarsal claw with small or large inner tooth. Forewing with base of vein $2A + 3A$ and $2r$ absent, $2r-m$ present; hindwing with anal cell present. Female with 9th abdominal segment extremely enlarged and wide ventrally; cerci about as long as sheath; ovipositor strongly sclerotized and strong; dorsal teeth on apical third of lance, that on 6th annulus largest, and 5th and 6th annuli with laterally protruding ridges; ventral teeth on apical half of lancet from 5th annulus to apex and a laterally protruding ridge on 5th annulus. Wings hyaline. Male with apical sternite slightly emarginate at apex and 8th tergite produced into a broad, rounded lobe; forewing with basal $\frac{2}{3}$ lightly black infuscated, apex beyond stigma hyaline.

Discussion.—*Nematus* was the name applied to this group of species by Konow (1905) and others prior to Rohwer (1911). In his work on the type species of Symphyta, Rohwer (1911) fixed the type of *Nematus* as *Tenthredo septentrionalis* L. as well as the type of the genus *Croesus* as *Tenthredo septentrionalis*, thus making these two genera synonymous. *Nematus* Panzer, however, is monotypic with the type species *Tenthredo (Nematus) lucidus* Panzer, and *Nematus* and *Croesus* are currently considered separate genera. This left the group considered by Konow (1905) without a name, and Rohwer stated "For *Nematus* Konow and authors the name *Nematinus* may be used," and he designated the type as *Tenthredo abdominalis* Panzer.

The obvious recognition characters for *Nematinus* are the enlarged ninth abdominal segment, sheath, and ovipositor of the female. Disregarding these specialized structures, the relationships of members of this genus to other members of the Nematinae are difficult to determine and must wait an analysis of all the nematine genera. The evenly tapered left mandible and non-differentiated mesal and lateral flaps of the male valve exclude this group from the "specialized" Nematinae (*Pachynematus*, *Pristiphora*, *Nematus*, etc.) of Ross (1937). These characters are more similar to the more primitive genera such as *Hemichroa*, *Anoplonyx*, and *Fallocampus*, all of which, however, are separated by the presence of the base of vein $2A + 3A$ and the usual presence (except *Fallocampus*) of vein $2r$ in the forewing. *Nematinus* may occupy an intermediate position between the more specialized and primitive genera of the subfamily.

The enlarged ninth abdominal segment resembles that of *Decanematus*, a genus that belongs in the specialized Nematinae of Ross (1937). *Decanematus* is separated by the constriction of the left mandible separating the bulbous base and the apical blade, the sheath being two times or more longer than high in lateral view and of uniform thickness in dorsal view, the cerci which are shorter than the sheath, the lack of dorsal teeth on the lance, and the presence of serrulae the full length of the lancet (Wong, 1968).

The following key is for Nearctic females. The male is described only for *unicolor* from a specimen from New Hampshire. I have also seen males from Michigan, Minnesota, Maine, and Wisconsin, none of which differ appreciably from the description of *unicolor*. Due to possible wear of the ovipositor, the teeth of the lance and lancet of some specimens may not always appear as sharp as in the illustrations.

KEY TO SPECIES

1. Inner tooth of tarsal claw small, much shorter than outer tooth and located near center of claw (Fig. 3) (small, 5.0–6.5 mm; head mostly orange, thorax with prescutum and mesosternum black, abdomen orange with terga black, except apical 2 or 3) *pontanioides* (Marlatt)
- Inner tooth of tarsal claw long, nearly as long as outer tooth and usually located closer to and parallel with outer tooth (Fig. 4) 2
2. Dorsum of head, mesonotum, mesosternum and dorsum of abdomen mostly black; hindocelli farther apart than distance from hindocelli to posterior margin of head, as 1.0:0.7 *parsebenus*, n. sp.
- Orange, at most black marks on lateral lobes of mesonotum and occasionally terga 1–6 or 7; distance between hindocelli subequal to distance from hindocelli to posterior margin of head, as about 1.0:1.0 3
3. Orange with black marks usually present on lateral lobes of mesonotum; area between dorsal teeth of 5th and 6th annuli of lance low and straight (Fig. 7); 5th segment of lancet nearly quadrate (Fig. 8) *unicolor* (Marlatt)
- Orange, basal terga sometimes blackish; area between dorsal teeth of 5th and 6th annuli of lance deep and concave (Fig. 11); 5th segment of lancet higher than long (Fig. 12) *ochreatus* (Rohwer)

Nematinus ochreatus (Rohwer)

Figs. 11, 12

Pteronus ochreatus Rohwer, 1910: 198.*Nematinus ochreatus*: Ross, 1951: 37; Smith, 1979: 56.

Female.—Length, 5.0–7.0 mm. Orange, narrow margins around each ocellus and dorsal margins of cervical sclerites blackish; sometimes very light stripes on lateral lobes of mesonotum and medial portion of terga 1–6 or 7 blackish. Distances between eye and hindocellus, between hindocelli, and between hindocellus and posterior margin of head as 1.0:0.8:0.8. Tarsal claw with long inner tooth. Lance with dorsal tooth of annulus 6 large, area between teeth of 5th and 6th annuli rounded, concave; 5th segment of lancet higher than broad.

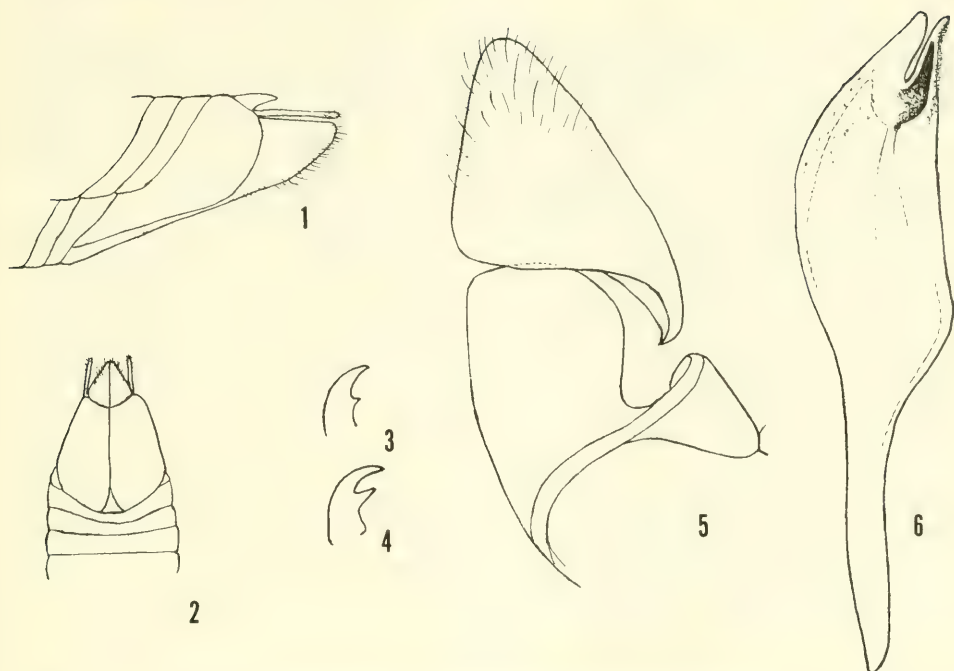
Male.—Unknown.

Type.—In USNM, female, labeled “St. John, N.B., 14 Jul.,” “A. G. Leavitt, Collector,” “Type No. 12022 U.S.N.M.,” “*Pteronus ochreatus* Roh., type.”

Host.—One specimen from Mabel Lake, B.C., was reared from *Alnus*.

Distribution.—British Columbia: Mabel Lake, 22-VII-50, *Alnus*. California: Echo Lake, El Dorado Co., VI-25-1954. Colorado: “Colo.” New Brunswick: Edmundston, VII-19-1970; St. John, VII-14; Bathurst, VII-9. New York: Keene Valley, VI-20-1894 (labeled as a paratype of *unicolor*). Oregon: Mt. Hood; S. entrance Crater Lake N. P., VI-24-1956; Baker Co., Velvet Cr., 28 mi. SE Union, 4720', VI-22-28-1975. Ontario: Sand Lake, VI-28-1926. Utah: Grand Co., VI-11-1963. Washington: Yakima, VI-1-1931. Wyoming: Woods Landing, Laramie R., VI-28-1948.

Discussion.—The mostly orange coloration, long inner tooth of the tarsal claw, concave area between segments 5 and 6 of the lance, and subequal distance between the hind ocelli and posterior margin of the head will separate *ochreatus*. The color is similar to that of *unicolor*, but characters of the ovipositor (compare



Figs. 1-6. 1, Lateral view of apex of abdomen and sheath of *Nematinus unicolor*. 2, Same, ventral view. 3, Tarsal claw of *N. pontanioides*. 4, Tarsal claw of *N. unicolor*. 5, Male genital capsule, ventral view of left side, of *N. unicolor*. 6, Valve of *N. unicolor*, lateral view, dorsal edge at left.

Figs. 7, 8, 11, 12) and generally smaller size of *ochreatus* (5.0–7.0 mm long compared to 6.7–8.0 mm long) will separate the two.

Nematinus parsebenus, NEW SPECIES

Figs. 13, 14

Female.—Length, 5.5–7.0 mm. Antenna blackish, more brownish from 4th segment to apex. Head orange to red brown, large area on top from and including postocellar area to interantennal area and extending laterally to near inner margins of eyes black. Thorax orange to red brown with cervical sclerites, mesosternum, large spots on mesoprescutum and lateral lobes of mesonotum, and sometimes mesepisternum black. Abdomen orange to red brown with terga black except for apical 2 or 3 segments. Legs orange; coxae black at bases; all coxae, femora, and apex of hindtibia may be black. Wings hyaline, costa and stigma amber, veins brownish. Hindocelli close to posterior margin of head; distances between eye and hindocellus, between hindocelli, and between hindocelli and posterior margin of head as 1.0:1.0:0.7. Tarsal claw with long inner tooth. Lance with dorsal tooth of annulus 6 large, area between teeth of 5th and 6th annuli deeply concave. Lancet with 5th segment higher than broad.

Male.—Unknown.

Type.—Female, Cape Breton Highlands National Park, Nova Scotia, labeled “N.S.C.B.H.N.P., 60°44'W, 46°48'N, 6-VI-1983, Maple PG732858.” In the Canadian National Collection, Ottawa.

Paratypes.—Maine: Katahdin, VII-8-1958 (1 ♀). New Hampshire: Bretton Woods, VII-5-1927, S. A. Shaw (1 ♀). Nova Scotia: Same data as for holotype except dates, VII-1-1983 (1 ♀), VI-22-1983 (1 ♀). Quebec: Thunder River, VI-19-1930, W. J. Brown (1 ♀); Bradore Bay, VII-25-1929, W. J. Brown (1 ♀); Indian House Lake, VII-19-1954, W. R. Richards (1 ♀). Deposited in the Canadian National Collection, Illinois Natural History Survey, and USNM.

Discussion.—This is a small species, close to *ochreatus*, but there are two consistent features that separate *parsebenus*: the hindocelli are much farther apart than their distance from the posterior margin of the head and the tooth of the sixth annulus of the lance is larger and broader (compare Figs. 11–14). In addition, this is a darker species with more black on the dorsum of the head, dorsum and venter of the thorax, and sometimes the legs; *ochreatus* is essentially all orange yellow.

Variation is noted, especially in the amount of black on the thorax and legs. The specimens from Cape Breton are darkest with most of the mesonotum, mesepisternum, mesosternum, femora, and apex of hindtibia black. Other specimens have the mesepisternum, mesoscutellum, and most of the legs orange to red brown.

The name refers to the partly black coloration of this species, a much darker species than the other North American ones.

Nematinus pontanioides (Marlatt)

Figs. 3, 9, 10

Nematus pontanioides Marlatt, 1896: 89; Konow, 1905: 63; Cresson, 1928: 8.

Nematinus pontanioides: Ross, 1951: 37 ("eastern"); Burks, 1958: 13 (Oreg., not eastern); Smith, 1979: 56.

Pachynematus oronus Kincaid, 1900: 347. New synonymy.

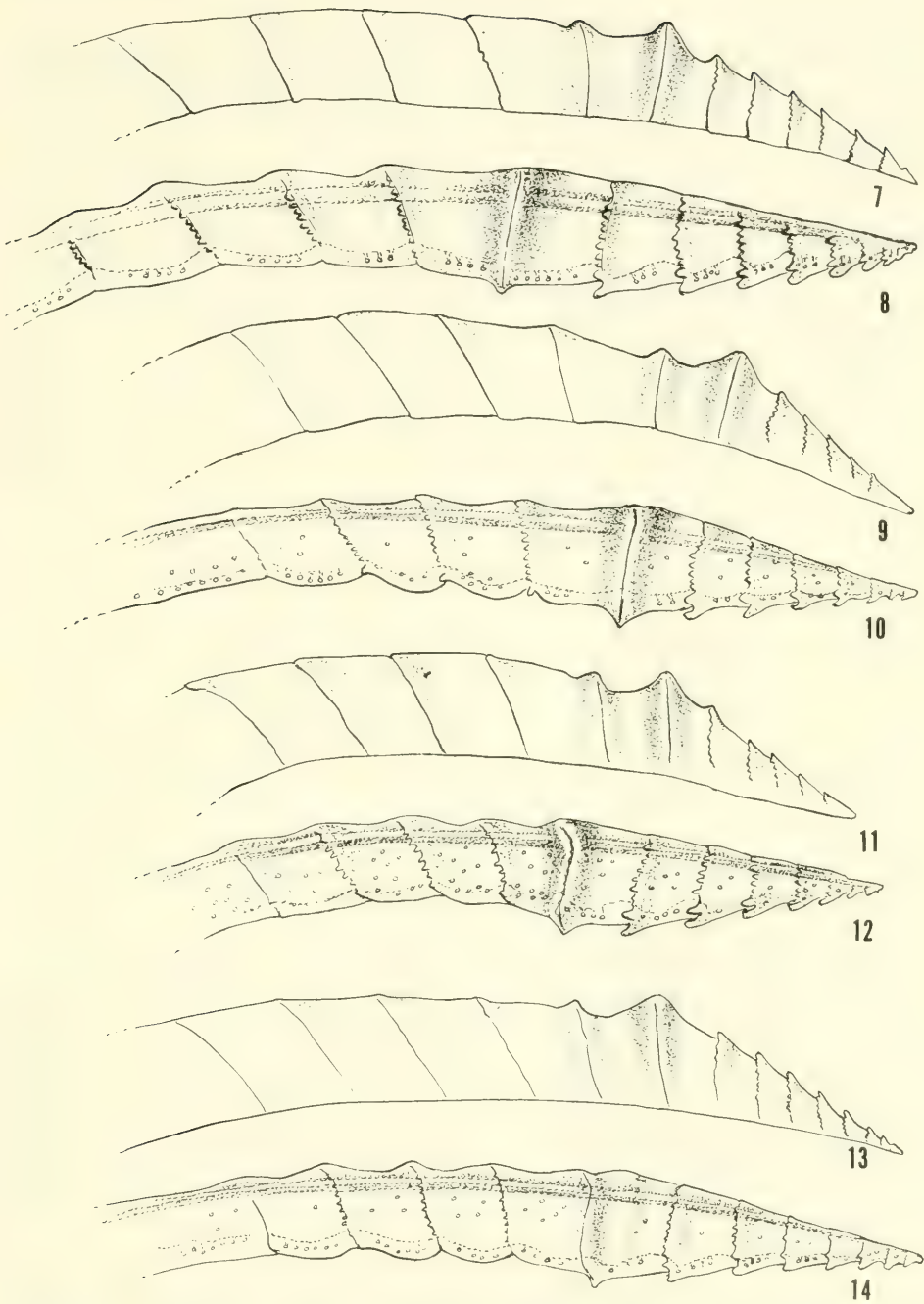
Nematinus oronus: Ross, 1945: 120; Ross, 1951: 37; Smith, 1979: 56.

Female.—Length, 5.0–6.5 mm. Antenna blackish, apical 3 or 4 segments reddish brown; base of scape reddish brown. Head orange to reddish brown with ocellar area and sometimes area immediately surrounding ocelli black. Thorax orange to reddish brown with cervical sclerites, usually mesoprescutum, mesosternum, mesepimeron, and metapleuron black. Abdomen orange to reddish brown with most of terga except apical 2 or 3 black. Legs orange to reddish brown with bases of coxae black; tibiae more whitish than darker orange femora and tarsi. Distances between eye and hindocellus, between hindocelli, and between hindocelli and posterior margin of head as 1.0:0.8:0.8. Tarsal claw with minute inner tooth, much shorter than outer tooth and located near center of claw. Tooth of 6th annulus of lance large, area between teeth of 5th and 6th annuli deeply concave.

Male.—Unknown.

Types.—*N. pontanioides* Marlatt, ♀, labeled "Mt. Hood, Oregon," "T. No. 10248" is in the Academy of Natural Sciences of Philadelphia (Cresson, 1928). *P. oronus* Kincaid, ♀, labeled "Yakutat Bay, Alaska, June 21, 1899," "Type No. 5285 U.S.N.M." is in the USNM; this is one of the 3 females Kincaid had, all with the same data, and is hereby designated lectotype.

Distribution.—Alaska: Same data as for lectotype of *oronus*; Curry, VI-28-1952; on tundra, Naknek, VII-3-1952, VII-8-1952; Muir Inlet, Glacier Bay, VI-26-1965. British Columbia: Emerald Lake, VI-12-1970; Forbidden Plateau, Vancouver Is.,



Figs. 7-14. Ovipositors. 7, Lance, and 8, lancet of *Nematinus unicolor*. 9, Lance, and 10, lancet, of *N. pontanioides*. 11, Lance, and 12, lancet of *N. ochreatus*. 13, Lance, and 14, lancet, of *N. parsebenus*. All are drawn to the same scale.

VII-13-1935, 6000'. Oregon: Linn Co., Monument Peak Guard Station, VII-17-1969; Monument Peak summit, 8 mi ESE Gates, 4725', VI-16-1960; 5 mi W Suttle Lake, VII-8-1939; Mt. Hood. Washington: Bald Knob Campground, Mt. Spokane State Park, Spokane Co., 4800–5200', VII-6-1978, sweeping; Seattle, UW campus, 1945; Stevens Co., Deer Lake nr. Chewelah, V-27-1973.

Discussion.—The small inner tooth of the tarsal claws and the black on the ocellar area, mesoprescutum, mesosternum, and terga are distinctive for this species. Two specimens, the type of *pontanioides* and the specimen from Seattle, Wash., are slightly darker with most of the thorax blackish. This species is primarily northern with southern extensions in the Cascades and northern Rockies; most of the southern specimens were taken at high altitudes.

Marlatt (1896) stated the following regarding the name he proposed: “. . . long sharply pointed sheath and long cerci may indicate a gall-making habit, whence the designation *pontanioides*.” Though nothing is known of its habits, it is probably a leaf feeder rather than a gall former.

***Nematinus unicolor* (Dyar)**

Figs. 1, 2, 4–8

Nematus unicolor Dyar, 1895a: 308; Dyar, 1895b: 340; Marlatt, 1896: 88; Konow, 1905: 63.

Nematinus unicolor: Ross, 1937: 82–83; Ross, 1951: 37; Wong, 1951: 65; Wong, 1954: 154–158; Burks, 1958: 13; Smith, 1979: 56.

Female.—Length, 6.7–8.0 mm. Orange with black streaks on lateral lobes of mesonotum; pronotum, tegula, clypeus, malar area, and tibiae paler, more whitish than orange on rest of body. Wings very faintly yellowish. Distances between eye and hindocellus, between hindocelli, and between hindocelli and posterior margin of head as 1.0:0.8:0.9. Tarsal claw with long inner tooth. Dorsal tooth of 6th annulus of lance rather small, low, area between teeth of 5th and 6th annuli shallow, nearly straight; 5th segment of lance nearly quadrate.

Male.—Length, 5.0 mm. Head orange with large black area on dorsum surrounding ocelli and extending nearly to antennal insertions and inner margins of eyes. Thorax orange with prescutum and lateral lobes of mesonotum, dorsal half of mesepimeron, mesosternum, and metanotum between cenchri and metascutellum black. Abdomen reddish brown with terga 1 and 2 black. Legs reddish brown with only extreme bases of coxae black. Forewing blackish infuscated to about stigma, hyaline apical to stigma. Hypandrium slightly emarginate at apex. Valve without differentiated mesal and lateral flaps, apex divided into 2 small membranous lobes and lateral face with sclerotized spur (Fig. 6); ventral view of genital capsule as in Fig. 5.

Type.—Female, labeled “4J,” “reared from larvae on white birch, H. G. Dyar coll.,” “Type No. 3492 U.S.N.M.,” “*Nematus unicolor* Marlatt, type.” Dyar’s “4J” rearings are from Keene Valley, N.Y. A type was not designated and there are 5 females in the USNM labeled “4J.” The one labeled as above is designated lectotype.

Distribution.—British Columbia: Summit Lake, mi 392 Alaska Hwy., VI-29-30-1959, 4500'; Barkerville, VI-29-1948, on snow 6000'. Maine: Orono, VII-16-1913. Manitoba: (Wong, 1954). Michigan: Marquette. Newfoundland: Corner Brook, VIII-1967. New Hampshire: Hanover; Mt. Washington, 5300', VII-25-

1971; Hampton, VI-11-1919, VI-5-1908, VI-7-1906. New York: Keene Valley ("4J"); Cranberry Lake, VI-15-1925. Nova Scotia: Tabusintac, VI-II-1939; Cape Breton Highlands National Park, 60°50'W, 46°47'N, VII-1-1983, birch PG666829. Ontario: Constance Bay, white birch, III-9-1948; P. Arthur, white birch, em. III-20-1944; Steenbaugh, white birch, III-8-1951, III-1-1951. Quebec: Covey Hill, VI-28-1923; Lanoraie, VI-20-1915. Saskatchewan: (Wong, 1954). South Dakota: Harney Peak, VII-19-1924.

Host and biology.—Reared from white birch, *Betula papyrifera* Marsh. Dyar (1895a) stated that the larva sits flat on the surface of the leaf or is curled spirally; on maturing the larva enters the ground and forms a compact dark brown cocoon. He indicated the eating habits are as those of the "preceding" (species described) which he described as being solitary, on the underside of the leaf eating only the lower epidermis and parenchyma until nearly full grown, at which time they eat nearly the full leaf. Wong (1954) included the larva in a key to sawfly species feeding on white birch. He found larvae from the early part of July into September and October as solitary feeders feeding flat on the leaf and eating holes through it. They formed cocoons in the litter or topsoil for overwintering. There is one generation a year. The larva lacks caudal protuberances (present in *Nematus* and *Croesus* larvae) and the shape of the body is tadpole-like. Wong (1951) described the cocoon as being cylindrical with double walls, an outer wall of dull, loosely constructed coarse silken strands with earth and sand incorporated and adhering to it, and an inner wall that is shining and leather-like.

Discussion.—On the average, this is the largest species of *Nematinus* in North America (compare lengths of other species). The nearly entirely orange coloration, long inner tooth of the tarsal claws, and nearly flat area between the dorsal teeth of the 5th and 6th annuli of the lance are characteristic.

Ross (1937) described the male, associated with *unicolor* by females taken at the same locality (Hampton, N.H.). I regard this as the male though I have not seen specimens associated by rearings. All reared specimens I have seen are females.

Though attributed to Marlatt in the literature prior to 1979, Dyar's (1895a, b) description of the larva precedes Marlatt's (1896) description. Marlatt described the female from the series reared by Dyar ("Green Valley" in Marlatt must be an error for "Keene Valley") and also included one female from Mt. Hood, Oreg. The female from Mt. Hood is *N. ochreatus*. Though it was not described by Dyar, I regard the adult as lectotype. I could not find larvae and the adults are essentially part of the type series even though a different life stage. Dyar (1895a) did not intend to take credit for the species, indicating "Marlatt MS"; it was his intent to describe only the larva even though he must have had reared adults at hand.

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WHITE PAINTED SURFACES AS A SUBSTRATE FOR RESTING
AND OVIPOSITION IN *TABANUS RUBIDUS* WIEDEMANN
AND RELATED HORSE FLY SPECIES (DIPTERA: TABANIDAE)
ON A DAIRY FARM IN SOUTHERN CHINA

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Abstract.—Cylindrical and rectangular white painted posts in dairy barns were preferred over black or dark substrates for resting and oviposition, respectively, in four species of Tabanidae affecting Holstein cattle in a confinement dairy operation outside of Guangzhou in the Guangdong Province of southern China. *Tabanus rubidus* Wiedemann, *T. mandarinus* Schiner, *T. crassus* Walker, *T. calidus* Walker, *T. striatus* Fabricius and *Chrysops sinensis* Walker were observed feeding on the white areas of the body of the dairy cattle. Flies were not observed to rest or feed on the black areas of the cow. *Tabanus rubidus* was also seen feeding on water buffalo, *Bubalus bubalis*, which were maintained in the open and were of a slate gray skin color. In North America many scientists have reported the attraction of horseflies to black objects but our observations, even though preliminary, suggest that white as opposed to black is the preferred color for attracting Tabanidae in southern China.

Insects affecting livestock in China have not received as much research attention in recent years when compared with the current emphasis underway on insect pests that affect agricultural crops or forest reserves. The writers were concerned about the paucity of published information available regarding livestock when some accounts report low or non-economic population levels of insect pests (C.S.C.P.R.C., 1977). In neighboring countries insects as well as acarine pests can be of economic significance. Mitzmain in the Philippines (1913, 1916) discussed the transmission of *Trypanosoma evansi* by several species of Tabanidae that can cause surra. This disease affects horses, camels and dogs and often the parasite appears as a non-pathogenic infection in cattle and buffalo. An outbreak of *T. evansi* affected buffaloes in N.E. Thailand in 1982 (Lohr et al., 1985) and local veterinarians in southern China indicated a large number of water buffaloes and a smaller number of dairy cattle suffered from this disease in 1984. The authors felt that population levels of horse flies were high enough in this area in 1985 to cause concern.

The observations made on the Tabanidae in this paper were undertaken on a government dairy farm outside of the city of Guangzhou in the Guangdong Province of southern China from May 17 to June 6, 1985. Approximately 900 Holstein

dairy animals are maintained under partial confinement conditions in separate units composed of 100 cows each. Four of the units were completely enclosed with only large unscreened windows (63.5 × 95.2 cm) and open doorways (1 m in width) permitting access by flies and other pests. Five of the units containing lactating dairy animals were without sides and only white posts or pillars supported a roof. Shade cloth or screening to form an awning was provided on the side exposed to greatest intensity from the sun. Mature lactating dairy animals were maintained in approximately six of these open units, while one closed unit contained non-lactating animals and another closed unit the calves. An exercise yard located adjacent to each unit provided a release from their stalls for the night and the cattle were then returned to their stalls in the morning. Antibacterial or germicidal treatments were applied to the exercise yards biweekly and insecticide in the form of dichlorvos was applied on a weekly basis to eliminate bacterial and insect pests. An examination of the manure in the yard did not reveal any developing flies or other dung fauna, which can be attributed to the fact that the cattle were allowed the freedom of the exercise yard at night when many of the common manure-inhabiting fly pests such as the house fly, *Musca domestica* (L.), or stable fly, *Stomoxys calcitrans* (L.), are inactive.

The cattle were scrubbed down daily and their wastes washed out of the barns with running water. This process diluted manure which entered mud lined canals where the surrounding soil was enriched for growth of elephant grass (*Pennisetum purpureum*) and maize. These mud lined canals provided what appeared to be ideal developing sites for tabanid larvae. Mature elephant grass was cut daily and provided to the cattle. A sizeable work force of approximately 200 staff allowed these intensive labor operations to be carried out with relative ease. Along with green vegetation the diet of dairy cattle was supplemented with crushed sweet potato, maize, soybean cake, bonemeal and a mineralized salt.

MATERIALS AND METHODS

The Manitoba (black ball) trap used in this study was similar in design to that of Easton (1982) except that a rubber volley ball was used as the target instead of a ball made of styrofoam. In preliminary experiments the ball was suspended from a metal tripod and darkened with black ink. In later trials the ball was painted white. A glass quart jar fitted with an inward projecting screen cone was attached to the apex of the tripod to hold the insects. Two small pieces of resin insect strip placed inside the jar provided an insect kill. Dry ice in a powder form and wrapped in a newspaper was suspended from the tripod in later experiments to increase the catch.

The sticky-drum traps used in this study were similar to those of Thornhill and Hays (1972). Metal cans (26 cm in diameter and 66 cm in length) initially darkened with black ink were suspended near the ground so that the bottom of the can was approximately 30 cm above the substrate. In later experiments the cans were painted white. Transparent plastic wrap (0.5 mil) was applied to the drum and the surface covered with Tack Trap insect catching adhesive^c (Chicopee Mfg. Co., Everree, Georgia).

Ectoparasitic fly fauna were observed daily on three herds of Holstein dairy cattle as well as single water buffalo from May 17 to June 4.

Table 1. *Tabanidae* attracted to three types of traps on a dairy farm near Guangzhou (Guangdong Province) in southern China, 1985.

Date	White Cylinder	Black Cylinder ^a	Black Ball Trap
31 May 1985	2 ^c	1 ^b	0
1 June 1985	5 ^c	0	0
3 June 1985	13 ^c	0	0
4 June 1985	21 ^c	0	0

^a A sticky drum trap.
^b *Atylotus pallitarsis* (Olsufjev).
^c *Tabanus rubidus*.

RESULTS

Preliminary observations on livestock on this farm confirmed the presence of at least six species of tabanid, namely *T. rubidus* Wiedemann (15 females), *Tabanus striatus* Fabricius (1 female), *T. mandarinus* Schiner (4), *Tabanus crassus* Walker (1), *Tabanus calidus* Walker (3) and *Chrysops sinensis* Walker (2).

The Manitoba trap failed to capture any species of *Tabanidae* during the period of study from May 22 to June 4 even though numerous species of *Tabanus* were in evidence feeding on dairy cattle. Dry ice when used in conjunction with canopy traps permits an increase in the catch of insects that are blood feeding. The application of black ink to darken the canopy or shroud on May 26, however, failed to increase the effectiveness of this trap and the addition of dry ice wrapped in newspaper and suspended from the apex of the trap also was unsuccessful in attracting flies.

One female specimen of *Atylotus pallitarsis* (Olsufjev) was caught on a sticky black drum on May 22 while the trap was located approximately 20 yards from the cattle but no tabanid species were caught after the trap was moved into elephant grass approximately 400 m from cattle 2 days later.

Numbers of horseflies averaged 3–5 flies/water buffalo during any one period while 1–2 flies/animal were attracted to Holstein cattle in open doorways 1 m or greater in width.

Horseflies came into fly barns at larger windows only (window width >1 m or from open doorways). They landed only on the white portion of the cow. Flies were not observed resting or feeding on the black portions of the Holstein dairy cows and animals that were mostly black were not preferred as hosts. Flies preferred lighter areas particularly when the light color was in the area of the legs.

Female flies were noted to rest and oviposit on white surfaces, particularly pillars or posts that supported the roof of the open cattle units. No flies were noted resting on portions of the pillars or buildings painted black or areas that were soiled with cattle wastes. A search of the leaves of vegetation, namely elephant grass and maize, in the mud canals on the farm premises revealed no egg deposits. Several masses of eggs, however, were observed being laid by female flies on white pillars of the open dairy barns on May 28.

The drum was painted white on May 28 and placed near open cattle units. Table 1 indicates that the white surface as opposed to a black one was more attractive to tabanid species.



Fig. 1. Egg masses of *Tabanus rubidus*.

Ovipositional preference.—When first laid on white rectangular pillars, eggs were flat white in color and after 24 hours the egg masses became a dark grey. Approximately 205 eggs comprised each mass (Fig. 1) of 10 egg masses examined. Eggs laid on May 28 were observed to hatch on June 5 (after a 7 day period). Of three egg masses discovered on white portions of pillars on May 28, the heights the eggs were laid above the ground were 1.5, 2.1 and 3.0 m, respectively. On June 4 a total of 14 more egg masses were discovered among three livestock units. One egg mass examined was deposited 0.3 m above a cement surface, two egg masses were at a height of 1.5 m, four masses at 1.8, four masses at 2.1, one mass at 2.4 m, one mass at 3.0 m and one mass was deposited 3.7 m above the ground. The average height above the ground for the 14 egg masses was 2.0 m.

The repeated washing of waste materials below the egg masses provided a mechanism by which first instar larvae that reached water could easily be washed into the muddy canals where there was ample food material for their growth.

DISCUSSION

The negative results with blackened trap types were puzzling in view of the success that researchers in North America (Adkins et al., 1972; Cobb and Balsbaugh, 1976; Easton, 1982, 1983; Thorsteinson, 1958; Thorsteinson et al., 1964) have had with the Manitoba or canopy trap or the results Thornhill and Hays (1972) reported with the sticky black drum. In Manitoba, the glossy black sphere is believed to be more attractive to insects than other geometric shapes because more surface area reflects sunlight (Thorsteinson et al., 1964).

According to the Manitoba, Canada studies, visual clues are important if Tabanidae are strongly attracted to glossy black targets suspended in the Manitoba

trap. However, some species such as *Tabanus atratus* Fabricius or *Tabanus punctifer* Osten Sacken that feed on livestock in North America are apparently only rarely attracted by these visual cues because neither Cobb and Balsbaugh (1976) nor Easton (1982, 1983) were able to demonstrate the attraction of *T. atratus* or *T. punctifer* to either Manitoba or sticky drum traps in South Dakota.

Hansens et al. (1971) did report that a pattern of a white square on a black background on a sticky trap was superior to black alone for the collection of the salt marsh greenhead, *Tabanus nigrovittatus* Macquart, in New Jersey, USA; however, the Manitoba or Manning traps utilizing darkened targets were more effective than sticky traps in collecting this fly.

The background topography in which the trap is placed can be important. A difference in total numbers of flies or in fly species diversity from two traps of even an identical design may be due to background topography (R. Axtell, pers. comm.). The background topography on the prairie of the Northcentral Plains in North America is probably more uniform than in the semitropical forested areas of southern China. Manitoba, Manning, and other blackened trap types may be more effective in temperate climates and less effective in tropical areas where topography is more varied due to the greater flora diversity.

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THREE NEW SPECIES OF *TRICHOGRAMMA*
(HYMENOPTERA: TRICHOGRAMMATIDAE)
FROM NORTH AMERICA

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Abstract.—Three new species of *Trichogramma* from North America are described: *T. marthae* Goodpasture from Maryland and North Carolina, *T. meteorum* Vincent from Florida and *T. stampae* Vincent from Texas, Virginia, and Rioverde, Mexico. Illustrations, host records, distributions, and comparisons with similar species are provided.

Recent advances in *Trichogramma* taxonomy have made possible the identification of most of the known North American species. Nagarkatti and Nagaraja (1968) first demonstrated the usefulness of the male genitalia and antenna as sources for taxonomic characters of *Trichogramma*. Since then, Nagarkatti and Nagaraja have described four North American species (Nagaraja and Nagarkatti, 1973; Nagarkatti, 1975) and provided keys and species group assignments (Nagarkatti and Nagaraja, 1971, 1977) and many illustrations for 11 others. Pinto et al. (1978) provided keys for the common North American species and described two new species from that region. More recently (Platner and Oatman, 1981; Pinto and Oatman, 1985), six new species from North America were described. Pinto and others are currently working on a more comprehensive treatment of the North American *Trichogramma* to include illustrations and keys of all known species. A world key to species and species groups is given by Voegelé and Pin-tureau (1982).

Three new species of *Trichogramma* are described here to provide names for use in publications and other research communications by workers in Florida, Texas, North Carolina and Maryland, from whom much of the material was obtained, and to encourage the use of new taxonomic characters located on the flagellum of males or females of some species.

The descriptions are based on field-collected and laboratory-reared adults, preserved in alcohol, cleared in potassium hydroxide solution and mounted on glass microslides in balsam or Hoyer's medium. Rearing procedures followed those of Thorpe (1982). All laboratory cultures were maintained at 27°C, 70-80% RH, and constant light. Host eggs were *Heliothis virescens* (Fabricius). Description of color for *T. marthae* and *T. stampae* was based on freshly killed specimens from laboratory culture. For *T. meteorum*, only alcohol-preserved, field-collected ma-

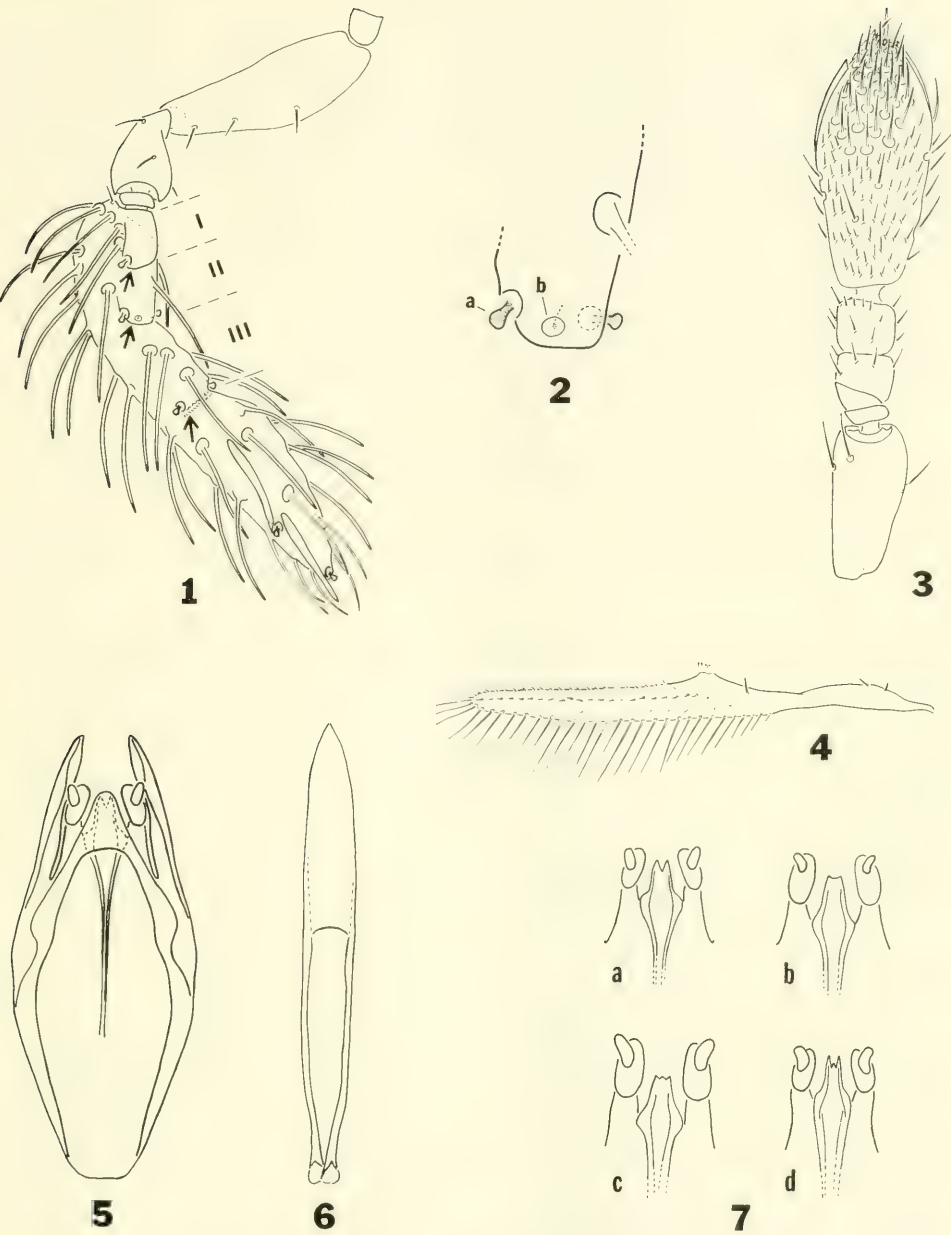
terial was available. Holotype quantitative data are presented separately as counts and ratios followed in parentheses by the measurements. Combined quantitative data for the male type series (including the holotype) are given in brackets and represent, in sequence, the mean, standard error, range, and sample size (N). Quantitative data for the female paratypes represent the range of counts or ratios followed in brackets by the mean, standard error, and sample size. On some paratypes, certain character-bearing structures are missing or obscured; thus, the sample size "N" is not the same for all characters measured. For the male genitalia (Fig. 17), we follow the terminology of Nagarkatti and Nagaraja (1968, 1971) with the exceptions listed by Pinto et al. (1978). However, we use the terms "scutellum" for the second dorsal sclerite on the mesothorax, and "flagelliform setae" for the longer, more numerous setae on the antenna of males, instead of the terms "mesoscutellum" and "flagellar setae," respectively, of Pinto et al. (1978). We prefer "scutellum" over "mesoscutellum" because in *Trichogramma* and most other chalcidoids the pronotum and metanotum are undifferentiated segmental plates; only the mesonotum shows differentiation into two sclerites. Thus, in our opinion it is unnecessary to use the prefix meso- with scutellum when indicating the posterior sclerite of the mesonotum. We prefer "flagelliform setae" over "flagellar setae" because here we use more than one type of seta on the flagellum for taxonomic characters. We feel that "flagelliform" more clearly refers to the shape of the individual setae rather than their location. Other terms used here for various types of antennal sensillae are trichoid seta, peg sensillum, campaniform sensillum, placoid sensillum, and apicoventral seta, which correspond respectively to sensillum types a, f, g, h, and i of Voegelé et al. (1975). In that paper, antennal structures of only female *Trichogramma* were described. However, except for apicoventral setae, similar structures are present on the flagellum of males of most *Trichogramma* species. Most of the terminology used in describing the male flagellum is given in Fig. 1. On males of some species, we have found that the presence, number, and location of the trichoid, peg, and campaniform sensillae have taxonomic value. Trichoid setae (shown in Figs. 8 and 14) are short, bristle-like setae on the venter of basoventral divisions I–III of males of some species. The number and location of placoid sensillae and numbers of apicoventral setae are used here as taxonomic characters for females only (shown in Figs. 3, 9, 10, 15, 16).

***Trichogramma marthae* Goodpasture, NEW SPECIES**

Figs. 1–7

Color.—Body of adult male golden yellow; dark brown on prothorax, scutum anteromedially, abdominal segments I and IV–VI laterally and II–III dorsally. Female similar to male except entire thorax yellow; grayish brown markings on abdomen weaker; tarsomere III on all legs dark brown.

Holotype male (male type series statistics in brackets).—Antenna (Fig. 1) with flagellum (excluding annellus) relatively long and curved, 0.21 as wide as long (0.033 and 0.162 mm) [0.19 ± 0.004 ; 0.16–0.23; N = 29], 1.08 as long as hindtibia (0.150 mm) [1.10 ± 0.012 ; 0.99–1.24; N = 29]; flagelliform setae relatively long and slender, tapering gradually from base to a more or less rounded apex, 71 in number [54.61 ± 2.402 ; 34–84; N = 28], the longest 1.61 as long as maximum width of flagellum (0.053 and 0.033 mm) [1.70 ± 0.031 ; 1.47–2.08; N = 28]; basoventral constrictions of flagellum strong; basoventral division I of flagellum



Figs. 1-7. *Trichogramma marthae*. 1, 2, 5-7, Male. 3, 4, Female. 1, Antenna. Arrow = basoventral constriction; numerals indicate basoventral divisions. 2, Basoventral division II; a = peg sensillum, b = campaniform sensillum. 3, Antenna (ventral view). 4, Hindwing. 5, Genital capsule (dorsal view). 6, Aedeagus. 7, Structural variation in the median ventral projection; a, b, d, lab reared specimens, c, field collected (Hexlena, Herford Co., North Carolina).

with 1 peg sensillum on the outer apicolateral angle, II-III with 1 peg sensillum on both apicolateral angles, II with a campaniform sensillum apicomediaally (Fig. 2).

Forewing vein tracts well defined, area between 4th and 5th vein tracts with 14 setae [13.56 ± 0.798 ; 8-24; N = 27]; longest seta on post-apical margin 0.145

as long as maximum width of wing (0.037 and 0.254 mm) [0.15 ± 0.004 ; 0.11–0.20; $N = 26$].

Hindwing (as in Fig. 4) posterior vein tract extending apically ca. $\frac{1}{2}$ the distance of the middle tract [range of paratypes $\frac{1}{3}$ – $\frac{2}{3}$], anterior tract composed of 2 setae [range of paratypes 2–4] and extending apically ca. $\frac{1}{3}$ the distance of the middle tract [range of paratypes $\frac{1}{6}$ – $\frac{1}{3}$], component setae of posterior and anterior tracts smaller than those of middle tract.

Scutellum with anterior seta 0.14 as long as posterior seta (0.005 and 0.033 mm) [0.18 ± 0.009 ; 0.13–0.26; $N = 27$].

Genital capsule (Fig. 5) 0.42 as wide as long (0.046 and 0.109 mm) [0.43 ± 0.004 ; 0.39–0.49; $N = 28$]; DEG tapering to a rounded apex, sides weakly concave, base strongly constricted; DEG extending 0.89 (0.097 mm long) [0.87 ± 0.003 ; 0.83–0.90; $N = 28$], CS extending 0.90 (0.099 mm long) [0.89 ± 0.003 ; 0.85–0.92; $N = 28$], and MVP extending 0.88 (0.096 mm long) [0.84 ± 0.003 ; 0.82–0.88; $N = 28$] the length of the genital capsule; MVP broad, apex notched, notch with small median tooth on 13 of 28 specimens (Fig. 7); aedeagus 0.76 (0.114 mm long) as long as hindtibia [0.80 ± 0.009 ; 0.73–0.93; $N = 28$], 1.04 as long as genital capsule [1.04 ± 0.010 ; 1.00–1.23; $N = 28$]; apodemes (0.06 mm long) comprising 0.54 [0.51 ± 0.007 ; 0.43–0.58; $N = 28$] the length of the aedeagus (Fig. 6).

Female (mean, standard error, and number of paratypes measured are in brackets).—Antennal club (Fig. 3) with 29–38 apicoventral setae [33.50 ± 1.936 ; $N = 4$] arranged in 8–9 [8.50 ± 0.289 ; $N = 4$] irregular transverse rows; placoid sensillae 5 in number, the most proximal extending basally to near midpoint of club length. Only two placoid sensillae are shown in Fig. 3 due to the ventral perspective.

Forewing area between 4th and 5th vein tracts with 6–25 [15.30 ± 1.181 ; $N = 30$] setae; longest seta on postapical margin 0.11–0.19 [0.14 ± 0.004 ; $N = 30$] as long as maximum width of wing.

Scutellum with anterior seta 0.13–0.35 [0.18 ± 0.010 ; $N = 29$] as long as posterior seta.

Ovipositor 1.12–1.45 [1.28 ± 0.013 ; $N = 30$] as long as hindtibia.

Type information.—Holotype δ reared from a laboratory culture established on 18-VI-1981, ex *H. virescens* egg cloth, collected on 11-VI-1981 from Beltsville, Prince Georges Co., Maryland, by Kevin W. Thorpe, mounted in balsam, deposited in the National Museum of Natural History (NMNH no. 77500); 64 paratypes (33 δ , 31 φ) in NMNH: 5 δ , 6 φ , same data as holotype; 26 δ , 20 φ reared from same laboratory culture as holotype, mounted in Hoyer's medium on 9–13-X-1982; 2 δ , 5 φ , mounted in balsam, reared from a *Lambdina pellucidaria* (Grote and Robinson) (Lepidoptera: Geometridae) egg, collected by A. T. Drooz, 24-IV-1980 on loblolly pine (*Pinus taeda* L.: Pinaceae) from Hexlena, Hertford Co., North Carolina.

Discussion.—According to Thorpe (1983), *T. marthae* (= his *T. sp. 4*) is reproductively isolated from *T. exiguum* Pinto and Platner, *T. pretiosum* Riley, and *T. minutum* Riley, based on crossing trials between *T. marthae* and various U.S. populations of these species. The morphology of the male genital capsule of this species corresponds to that of the minutum group of Voegelé and Pintureau (1982). Males of this species differ from those of other known North American

species of *Trichogramma* by the MVP apex which ranges from notched to arcuately emarginate (Fig. 7). On ca. 50% of males, the notch has a small median tooth (Fig. 7, c, d). *Trichogramma exiguum* and *T. fuentesi* Torre are similar to *T. marthae* in terms of most other male genital characters, coloration, and the general appearance of the flagellum of males. However, on *T. marthae*, the sides of the DEG narrow less abruptly (compare to Figs. 4, 5, Torre, 1980 and Fig. 1, Pinto et al., 1983) and the flagelliform setae of males taper less abruptly (compare to Fig. 3, Pinto et al., 1978) at their apex than on *T. exiguum* or *T. fuentesi*. Also, on the flagellum of males, *T. exiguum* has a peg sensillum on both apicolateral angles of basoventral division I, whereas *T. marthae* and *T. fuentesi* lack a peg sensillum on the inner apicolateral angle. On most specimens of *T. fuentesi*, the hindwing posterior vein tract extends to ca. $\frac{3}{4}$ the distance along the middle tract (Fig. 1a, Pinto et al., 1983), but on *T. marthae* it extends $\frac{1}{2}$ – $\frac{2}{3}$ the distance along the middle tract.

This species is named for Martha Grace, a personal friend.

Trichogramma meteorum Vincent, NEW SPECIES

Figs. 8–13

Color.—Body of adult male golden yellow; grayish brown on prothorax, scutum, coxae and tarsal segments III; abdominal segments II–III dark brown; pale yellow on legs except coxae and tarsal segment III. Female similar to male except entire thorax golden yellow; dark brown on abdominal terga II–III dorsally and IV–V laterally.

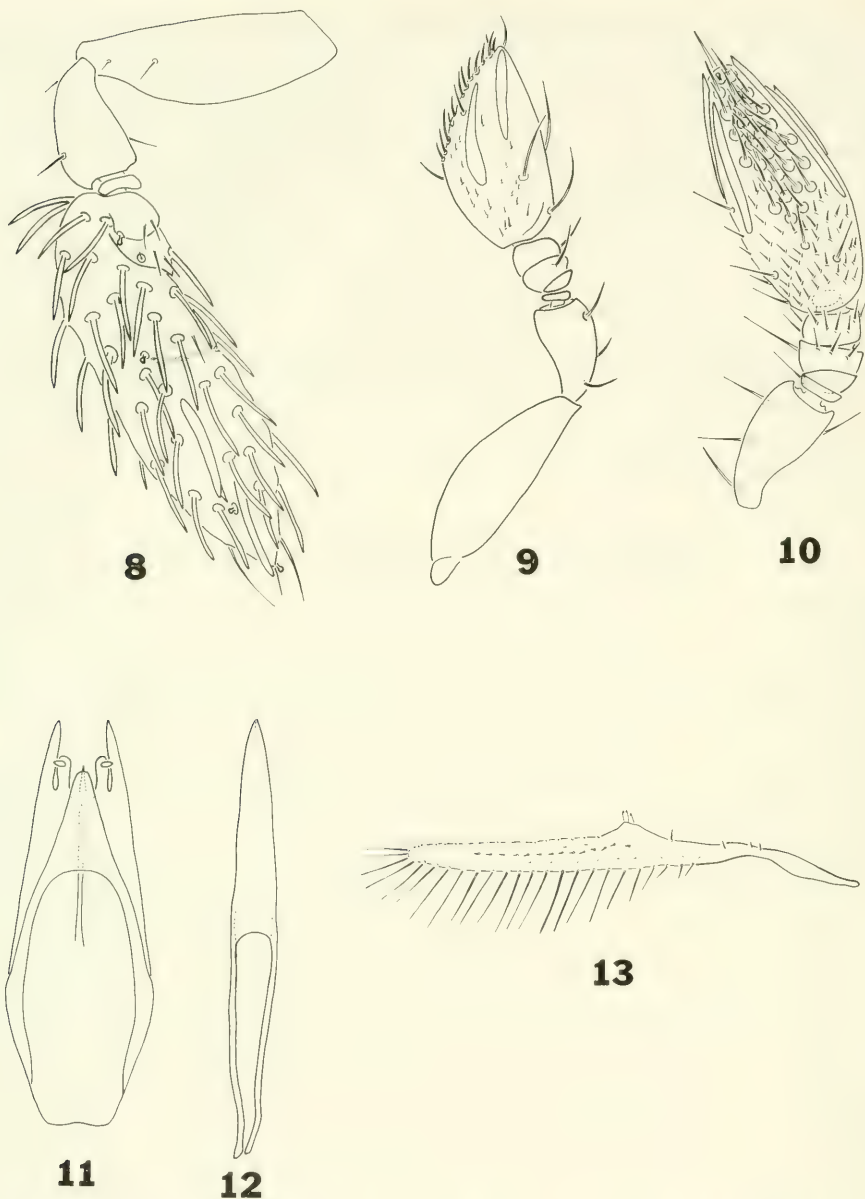
Holotype male (male type series statistics in brackets).—Antenna (Fig. 8) with flagellum (excluding annellus) relatively short and straight, 0.30 as wide as long (0.041 and 0.135 mm) [0.33 ± 0.006 ; 0.30–0.35; N = 8], 0.88 as long as hindtibia (0.153 mm) [0.89 ± 0.009 ; 0.85–0.93; N = 8]; flagelliform setae relatively short, stout, tapering abruptly at apex, 78 in number [60.69 ± 3.635 ; 47–78; N = 8], the longest 0.67 as long as maximum width of flagellum (0.027 and 0.041 mm) [0.70 ± 0.012 ; 0.65–0.75; N = 8]; basoventral constrictions of flagellum weak; basoventral divisions of flagellum with a few appressed trichoid setae, three on I–III together [5.33 ± 0.391 ; 3–7; N = 9], I and III each with one peg sensillum on the outer apicolateral angle, II without a peg sensillum but with a campaniform sensillum on outer apicolateral angle.

Forewing vein tracts well defined, area between 4th and 5th vein tracts with 13 setae [11.50 ± 2.363 ; 7–15; N = 3], longest seta on post-apical margin 0.13 as long as maximum width of wing (0.032 and 0.252 mm) [0.14 ± 0.007 ; 0.13–0.15; N = 3].

Hindwing (as in Fig. 13) posterior vein tract extending apically ca. $\frac{1}{2}$ the distance of the middle tract, anterior tract composed of two setae (range of paratypes 2–3) and extending apically ca. $\frac{1}{4}$ the distance of the middle tract, component setae of posterior and anterior tracts smaller than those of middle tract.

Scutellum with anterior seta 0.46 as long as posterior seta (0.013 and 0.029 mm) [0.35 ± 0.018 ; 0.30–0.46; N = 10].

Genital capsule (Fig. 11) 0.33 as wide as long (0.041 and 0.124 mm) [0.33 ± 0.011 ; 0.29–0.38; N = 7]; DEG tapering gradually to a rounded apex, sides weakly concave, base weakly constricted; DEG extending 0.86 (0.107 mm long) [$0.87 \pm$



Figs. 8-13. *Trichogramma meteorum*. 8, 11, 12, Male. 9, 10, 13, Female. 8, Antenna. 9, Antenna (lateral view). 10, Antenna (ventral view). 11, Genital capsule (dorsal view). 12, Aedeagus. 13, Hindwing.

0.007; 0.83-0.91; $N = 11$], CS extending 0.90 (0.112 mm long) [0.90 ± 0.006 ; 0.88-0.93; $N = 12$], and MVP extending 0.88 (0.109 mm long) [0.86 ± 0.006 ; 0.83-0.90; $N = 11$] the length of the genital capsule; MVP slender, apex acute; aedeagus (0.126 mm long) 0.83 as long as hindtibia [0.89 ± 0.015 ; 0.81-1.00; $N = 12$], 1.02 as long as genital capsule [1.02 ± 0.007 ; 0.99-1.07; $N = 12$]; apo-

demes (0.059 mm long) comprising 0.47 the length of the aedeagus (Fig. 12) [0.45 ± 0.005 ; 0.42–0.47; $N = 12$].

Female (mean, standard error, and number of paratypes measured are in brackets).—Antennal club (Figs. 9, 10) with 26–28 apicoventral setae [26.88 ± 0.515 ; $N = 4$] arranged in 7–8 [7.25 ± 0.164 ; $N = 8$] irregular transverse rows; placoid sensillae 5 in number, the most proximal extending basally to near midpoint of club length.

Forewing area between 4th and 5th vein tracts with 5–13 [10.18 ± 0.651 ; $N = 11$] setae; longest seta on post-apical margin 0.12–0.15 [0.13 ± 0.003 ; $N = 11$] as long as maximum width of wing.

Scutellum with anterior seta 0.30–0.48 [0.35 ± 0.015 ; $N = 19$] as long as posterior seta.

Ovipositor 0.91–1.01 [0.96 ± 0.007 ; $N = 19$] as long as hindtibia.

Type information.—Holotype ♂ reared from a *Dioryctria ebeli* Mutuura and Munroe egg (Lepidoptera: Pyralidae) collected 15–22 June 1979 on slash pine (*Pinus elliottii* Engleman: Pinaceae) from Olustee, Baker Co., Florida, by Robert A. Belmont, deposited in the National Museum of Natural History (NMNH no. 77498); 33 paratypes (13 ♂, 20 ♀) in NMNH with the same data as the holotype. This species is known only from the type locality.

Discussion.—Details of parasitism rates and other host/parasite information are given by Belmont (1979) and Belmont and Habeck (1983). The morphology of the male genital capsule (DEG not constricted at base, MVP well developed and forming a sharp point apically) of this species does not correspond well with any of the species groups of Voegelé and Pintureau (1982). Males of *T. meteorum* differ from those of most known North American species of *Trichogramma* by having very short, stout, flagelliform setae and by the presence of appressed trichoid setae on the basoventral divisions of the antennal club (Fig. 8). Males of *T. brevicapillum* Pinto and Platner (their Fig. 17, 1978), and *T. stampae* Vincent (new species, Fig. 17) are similar to *T. meteorum* in these respects. However, on males of *T. meteorum*, the DEG gradually tapers to a rounded apex which does not quite reach the apex of the CS, and the MVP is slender and gradually tapers to a sharp point apically (Fig. 11), compared to males of *T. brevicapillum* in which the DEG gradually tapers to a moderately acute apex which extends to the apex of the CS, and the MVP is blunt apically. Also, the forewing disc of *T. meteorum* is sparsely covered with setae arranged in well-defined vein tracts and the anterior and posterior vein tracts of the hindwing extend no more than $\frac{1}{2}$ the distance of the middle tract (Fig. 13), while on *T. brevicapillum* the forewing disc is densely covered with setae arranged in poorly defined vein tracts (area between the 4th and 5th vein tracts with 72.5 ± 3.0 ; 52–89; $N = 12$ setae; Pinto et al., 1978) and the anterior and posterior vein tracts of the hindwing extend to the wing apex (Fig. 9, Pinto et al., 1978). On males of *T. stampae* the antennal club has relatively strong basoventral constrictions, the flagelliform setae taper gradually from base to apex, the DEG is strongly constricted at its base, and the DEG and MVP extend to the CS apex. The antennal club of male *T. meteorum* has very weak basoventral constrictions, the flagelliform setae taper more abruptly at their apex, the DEG is not constricted basally, and the DEG and MVP do not extend to the CS apex. Living specimens of *T. meteorum* are golden to pale yellow with some grayish

brown markings on the thorax and abdomen, while specimens of *T. brevicapillum* and *T. stampae* are predominantly dark brown to black with a few pale areas on the head and legs.

The specific epithet *meteorum* is an adjective from the Greek *meteōros* meaning suspended or high in the air, and refers to the habitat of its only known host.

Trichogramma stampae Vincent, NEW SPECIES

Figs. 14–19

Color.—Body of adults dark brown; scutum, abdominal terga II–III black; pale yellow on vertex, antenna, and legs except grayish brown on tarsal segment III and hindfemur.

Holotype male (male type series statistics in brackets).—Antenna (Fig. 14) with flagellum (excluding annellus) relatively short and straight, 0.26 as wide as long (0.032 and 0.123 mm) [0.28 ± 0.005 ; 0.26–0.33; $N = 17$], 0.76 as long as hindtibia (0.162 mm) [0.77 ± 0.004 ; 0.73–0.80; $N = 17$]; flagelliform setae relatively short and slender, tapering gradually from base to apex, 42 in number [38.50 ± 0.868 ; 32–42; $N = 16$], the longest 1.27 as long as maximum width of flagellum (0.040 and 0.032 mm) [1.20 ± 0.015 ; 1.04–1.28; $N = 17$]; basoventral constrictions of flagellum strong; basoventral divisions of flagellum with several appressed trichoid setae, 13 on I–III together [11.38 ± 0.415 ; 8–14; $N = 16$], I–III each with 1 peg sensillum on the inner and outer apicolateral angle, II with a campaniform sensillum apicomediaally.

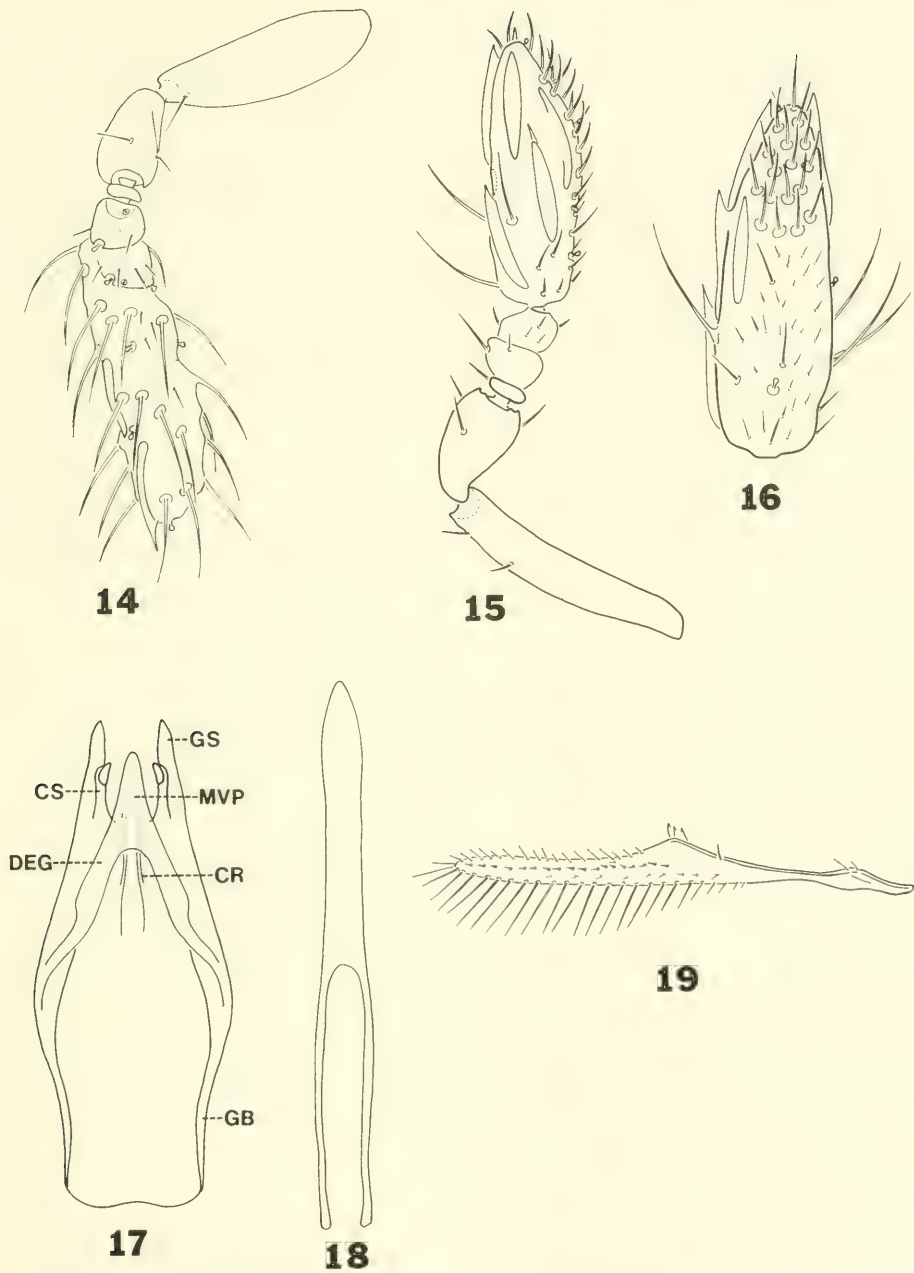
Forewing vein tracts well-defined, area between 4th and 5th vein tracts with 17 setae [13.38 ± 0.877 ; 8–18; $N = 3$]; longest seta on post-apical margin 0.17 as long as maximum width of wing (0.044 and 0.256 mm) [0.18 ± 0.302 ; 0.15–0.20; $N = 11$].

Hindwing (as in Fig. 19) posterior vein tract extending apically ca. $\frac{1}{2}$ the distance of the middle tract, anterior tract composed of 2 setae (range of paratypes 1–2) and extending apically ca. $\frac{1}{3}$ the distance of the middle tract, component setae of posterior and anterior tracts smaller than those of middle tract.

Scutellum with anterior seta 0.19 as long as posterior seta (0.007 and 0.037 mm) [0.21 ± 0.010 ; 0.16–0.30; $N = 14$].

Genital capsule (Fig. 17) 0.44 as wide as long (0.065 and 0.147 mm) [0.39 ± 0.015 ; 0.32–0.46; $N = 11$]; DEG tapering to a rounded apex, sides weakly concave, base strongly constricted; DEG extending 0.92 (0.135 mm long) [0.93 ± 0.004 ; 0.90–0.95; $N = 17$], CS extending 0.89 (0.131 mm long) [0.89 ± 0.005 ; 0.84–0.92; $N = 15$], and MVP extending 0.89 (0.131 mm long) [0.89 ± 0.005 ; 0.85–0.91; $N = 16$] the length of the genital capsule; MVP not tapering apically, apex rounded; aedeagus (Fig. 18) (0.170 mm) 1.05 as long as hindtibia [1.06 ± 0.010 ; 1.02–1.15; $N = 17$], 1.16 as long as genital capsule [1.14 ± 0.005 ; 1.10–1.18; $N = 17$]; apodemes (0.073 mm long) comprising 0.43 the length of the aedeagus [0.43 ± 0.007 ; 0.38–0.50; $N = 17$].

Female (mean, standard error, and number of paratypes measured are in brackets).—Antennal club (Figs. 15, 16) with 12–17 apicoventral setae [13.71 ± 0.286 ; $N = 21$] arranged in 4–6 [4.74 ± 0.154 ; $N = 34$] transverse rows; placoid sensillae 8 in number, raised, acute apically, the base of the most proximal sensillum extending basally to near the club base, the apex overhanging a shallow depression on club.



Figs. 14–19. *Trichogramma stampae*. 14, 17, 18, Male. 15, 16, 19, Female. 14, Antenna. 15, Antenna (lateral view). 16, Antennal club (ventral view). 17, Genital capsule (dorsal view)—(CR, chitinized ridge; CS, chelate structure; DEG, dorsal expansion of gonobase; GB, gonobase; GS, gonostyli; MVP, median ventral projection). 18, Aedeagus. 19, Hindwing.

Forewing area between 4th and 5th vein tracts with 15–33 [23.13 ± 0.531 ; $N = 57$] setae; longest seta on post-apical margin 0.13–0.18 [0.15 ± 0.001 ; $N = 57$] as long as maximum width of wing.

Scutellum with anterior seta 0.16–0.50 [0.27 ± 0.011 ; $N = 45$] as long as posterior seta.

Ovipositor 0.83–0.99 [0.93 ± 0.005 ; $N = 59$] as long as hindtibia.

Type information.—Holotype δ reared from a *Euphydryas phaeton* (Drury) egg (Lepidoptera: Nymphalidae), collected by Nancy E. Stamp, 12 July 1979 on turtlehead (*Chelone glabra* L.: Scrophulariaceae) from the Conservation and Research Center of the National Zoological Park, Front Royal, Warren Co., Virginia, deposited in the National Museum of Natural History (NMNH no. 77499); 76 paratypes in NMNH—9 δ , 59 φ with the same data as the holotype, and 8 δ from a laboratory culture reared on eggs of *Heliothis virescens* for 7 generations.

Additional material examined.—4 δ , 3 φ reared from eggs of *Chlosyne janais* (Drury) (Lepidoptera: Nymphalidae), collected by Roy A. Kendall, 27 October 1971 on *Anisacanthus wrightii* (Torr) Gray (Acanthaceae) from the Ebony Hill Research Station, San Antonio, Bexar Co., Texas; 45 δ , 145 φ reared from eggs of *Chlosyne ehrenbergi* (Geyer), collected by Roy A. Kendall, 12 March 1980 on *Buddleja sessiliflora* H.B.K. (Loganaceae) from Media Luna nr. Rioverde, San Luis Potosi, Mexico.

Discussion.—Details of parasitism rates and other host/parasite information given by Stamp (1981). The morphology of the male genital capsule of this species corresponds to that of the minutum group of Voegelé and Pintureau (1982). Males of *T. stampae* differ from those of most known North American species of *Trichogramma* by having very short flagelliform setae on the flagellum and by the presence of minute, appressed trichoid setae on the basoventral divisions of the club (Fig. 14). Males of *T. brevicapillum* and *T. meteorum* are similar in these respects. Details of the relative similarities and differences between males of these three species are given in the discussion under *T. meteorum*. Females of *T. stampae* differ from those of most other known *Trichogramma* species in having 8 placoid sensillae on the antennal club, the base of the most proximal sensillum extending basally to near the club base, the apex acute, raised, and overhanging a shallow depression on club.

This species is named for Nancy E. Stamp, who provided specimens from her study on parasitism of *E. phaeton* in Virginia (Stamp, 1981).

ACKNOWLEDGMENTS

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CHROMOSOMES OF TWO HYBRIDIZING SPECIES OF *LIMNOPORUS* (HETEROPTERA: GERRIDAE)

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Abstract.—Contrary to an earlier report (Calabrese and Talerico, 1984), *Limnopus notabilis* has a male diploid chromosome number of 21 and an XO male/XX female sex chromosome system. Thus, the cytology of *L. notabilis* is identical to that reported (Calabrese and Talerico, 1982) and confirmed in the present study for a closely related Nearctic species, *L. dissortis*. Male F_1 hybrids between *L. dissortis* and *L. notabilis* from both reciprocal crosses also have a diploid chromosome number of $2n = 20 + X$, and we observed no significant abnormality in meiotic behavior during hybrid spermatogenesis. Because of unusual meiotic behavior, careful study is required to determine the nature of sex chromosome systems in heteropterans. Data about composition of first and second metaphase chromosomes and comparison of chromosome counts from spermatogonial and oogonial mitosis are required to ensure correct interpretation.

Limnopus dissortis (Drake and Harris) and *L. notabilis* (Drake and Hottes) are related Nearctic water-striders that hybridize extensively in nature (Spence, 1981, and in preparation). *L. dissortis* occupies much of North America east of the Rocky Mountains (Brooks and Kelton, 1967), and *L. notabilis* ranges throughout the western U.S.A. and Canada (Polhemus and Chapman, 1979). In Canada, these species occur sympatrically along the eastern slopes of the Rockies and in central British Columbia. The zone of sympatry in central British Columbia is probably the result of a recent expansion of *L. dissortis* (see Scudder, 1977) and extensive introgression between the species is now occurring. Reproductive behavior (Wilcox and Spence, 1986; Spence and Wilcox, 1986) and patterns of interfertility among populations of these two species, as well as gene flow and geographic variation of structural and electrophoretic characters in western Canada, are presently under extensive investigation by one of us (JRS).

Calabrese and Talerico (1982, 1984) reported the chromosome complement of male *L. dissortis* as $2n = 20 + X$, and that of *L. notabilis* as $2n = 18 + XY$. Reports of these chromosomal differences between the two species appeared at odds with the extensive fertility of hybrids of the two taxa and their backcrosses noted in laboratory experiments (Spence, unpublished) and prompted us to reinvestigate the structure and number of chromosomes.

This paper presents observations on the chromosomes of *L. dissortis* and *L.*

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notabilis. In addition, we report on the chromosome complement and meiotic behavior of male F_1 hybrids between *L. dissortis* and *L. notabilis*.

MATERIALS AND METHODS

This paper is based on examination of fourth and fifth instar nymphs of both species and their hybrids. Adults of *L. notabilis*, collected from Marion Lake, near Haney, British Columbia, and those of *L. dissortis* from several small ponds near Swan Hills, Alberta were overwintered in the laboratory at 4°C. These bugs were used to establish laboratory breeding cultures and the resulting offspring were used in this study. Our results are based upon examination of chromosome squashes for 15 nymphs resulting from 7 laboratory crosses (*L. dissortis* and *L. dissortis* F $\times$ *L. notabilis* M, one cross each; *L. notabilis*, two crosses; *L. notabilis* F $\times$ *L. dissortis* M, three crosses). We studied additional squashes of 6 fifth instar nymphs collected from field populations of *L. dissortis* (Dunstable, Alberta) and *L. notabilis* (Fernie, British Columbia).

Gerrid nymphs were fixed in 95–98% ethanol : acetic acid (3:1), with or without prior (1–3 h) injection of 0.01% colchicine in an aqueous solution of 0.9% NaCl, 0.02% KCl, and 0.02% CaCl₂. The testes or ovaries were Feulgen-stained, squashed in 50% acetic acid, and remounted (using the dry ice technique) in Euparal® before observation. Photographs were taken with a Zeiss Photomicroscope I®, with phase contrast optics, using Kodak Panatomic X® film.

Chromosome number was determined for mitotic cells in both male and female preparations and for cells in both meiotic metaphases (MI and MII) in male preparations. When available, 10 well-squashed cells of each stage were counted for each bug; however, if variation in chromosome number was observed among the first 10 counts of any stage, we counted as many cells as possible. In addition, we studied the number of parts contained in each meiotic element. MI elements were either 2-parted or 4-parted, MII elements 1-parted or 2-parted. For all MI and MII cells for which the structure of every chromosomal element could be determined, the numbers of 1-parted, 2-parted, and 4-parted elements were recorded.

RESULTS

As is typical of heteropterans (Ueshima, 1979), *Limnoporus* chromosomes show no evidence of localized centromeres. As well, no m-chromosomes were observed. Sex chromosomes were positively heteropycnotic during meiotic prophase, especially in pachytene (Fig. 1).

Males of both *L. dissortis* and *L. notabilis* have 21 chromosomes (Fig. 2) while females have 22 (Table 1). At comparable stages in the cell cycle, we cannot distinguish between the chromosome complements of the two species. Mitotic chromosomes of both species are small and relatively uniform in size. The only distinctive element in mitotic metaphase is one slightly larger chromosome containing the nucleolar organizer; this chromosome occurs in both species (Fig. 2).

Both *L. dissortis* and *L. notabilis* have a male diploid number of 21 and an XO male/XX female sex chromosome system (Table 1). Female oogonial cells of both species consistently showed 22 chromosomes while mitotic spermatogonia of males showed only 21. In males of both species, meiotic cells in either MI or MII showed 11 elements, only one of which was 2-parted (MI) or 1-parted (MII) (Fig.

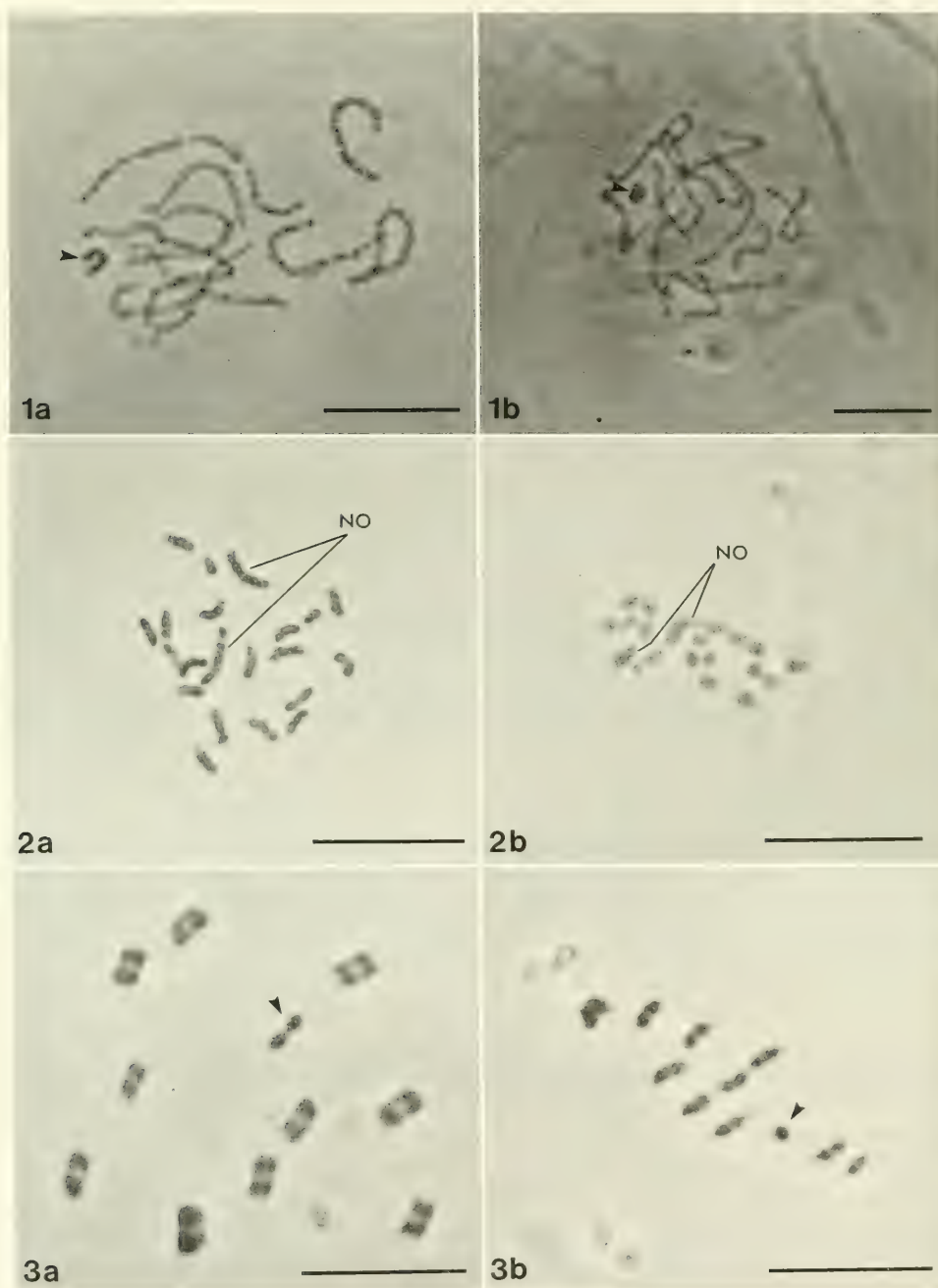


Fig. 1-3. 1, Male pachytene cells showing complete autosomal pairing and the condensed nature of the sex chromosome (X, indicated by arrows) in (a) *L. dissortis* (LIM-3B) and (b) an *F₁* hybrid (*L. notabilis* male × *L. notabilis* female, LIM-14). 2, Mitotic metaphase chromosomes of (a) male *L. dissortis* (LIM-3B) and (b) male *L. notabilis* (LIM-12). Chromosomes containing the nucleolar organizer indicated by NO. 3, Meiotic chromosomes of male *L. notabilis* (LIM-12), (a) Metaphase I, (b) Metaphase II. Arrows indicate the position of the X chromosomes. Scale bar = 10 μ m.

Table 1. Numbers of cells in which various chromosome counts were observed for specimens of *L. dissortis* and *L. notabilis* and their hybrids. Counts for females are from oogonial mitosis; those for males are from spermatogonial mitosis, and first (MI) and second (MII) metaphase of meiosis. Number of observed cells in which only one chromosome (presumably the X) was clearly 2-parted (MI) or 1-parted (MII) is given in parentheses; no cells with more than one such chromosome were observed, except in hybrids (see text for details).

Species and Sex	Locality	Chromosome Counts								
		Mitosis			MI			MII		
		20	21	22	10	11	12	10	11	12
<i>L. dissortis</i>										
F (LIM-6)	Swan Hills, AB	0	0	12						
M (LIM-5)	Swan Hills, AB	0	10	0	0	7 (6)	0	0	2 (2)	0
M (LIM-3)	Swan Hills, AB	0	10	0						
M (LD-8)	Dunstable, AB				0	10 (10)	0	0	10 (10)	0
M (LD-7)	Dunstable, AB	0	2	0	0	10 (10)	0	0	10 (10)	0
M (LD-5)	Dunstable, AB	0	3	0						
<i>L. notabilis</i>										
F (LIM-2)	Haney, BC	0	1	12						
F (LIM-19)	Haney, BC	0	1	22						
M (LIM-4)	Haney, BC	0	5	0	0	13 (13)	0	0	16 (14)	0
M (LIM-12)	Haney, BC	0	10	0	0	10 (7)	0	0	10 (9)	0
M (LN-41)	Fernie, BC	0	2	0				0	10 (9)	0
M (LN-40)	Fernie, BC	0	3	0	0	10 (10)	0	0	10 (9)	0
M (LN-34)	Fernie, BC				0	10 (10)	0			
Parents: <i>LDF</i> × <i>LMN</i>										
M (LIM-1)	lab reared	3	38	0	0	9 (9)	0	1	17 (16)	0
M (LIM-7)	lab reared	0	3	0						
M (LIM-16)	lab reared	0	10	0	1	28 (26)	0			
M (LIM-17)	lab reared	0	2	0						
Parents: <i>LNF</i> × <i>LDM</i>										
M (LIM-8)	lab reared	1	13	0	0	10 (10)	0			
M (LIM-9)	lab reared	0	10	0				0	3 (3)	0
M (LIM-11)	lab reared	0	2	0						
M (LIM-13)	lab reared	0	11	0	0	17 (16)	4	0	13 (11)	0
M (LIM-14)	lab reared	0	10	0	1	26 (24)	1	0	10 (7)	0

3). Data from hybrid males were also consistent with the hypothesis of an XO male/XX female sex chromosome system in both species (Table 1).

We also studied primary spermatocytes of F₁ hybrids for evidence of abnormal meiotic behavior. Chromosomal pairing during pachytene meiotic prophase seemed to be completely normal for hybrids (cf. Figs. 1a, 1b). In two of nine hybrid males (LIM-13 and LIM-14), a minority of metaphase cells were encountered with 12 distinct chromosomes rather than 11. However, for three of four such MI cells of LIM-13, it was clear that three chromosomes were only 2-parted, suggesting incomplete union of one autosomal pair during meiosis in some primary spermatocytes of hybrids. A few examples of anaphase II, encountered in hybrid slides representing both reciprocal crosses (LIM-1, 2 cells; LIM-13, 3 cells), were apparently normal showing no evidence of chromosomes fragmenting or lagging on the spindle. Overall, it appears that most meiotic behavior in hybrid males is normal and that there is no obvious chromosomal basis for expecting infertility in backcrosses involving these males.

DISCUSSION

Our results indicate that both *L. dissortis* and *L. notabilis* have $2n = 20 + X$ males and $2n = 20 + XX$ females. Thus, our study confirms Calabrese and Talerico's (1982) findings for *L. dissortis*, but disagrees with their (Calabrese and Talerico 1984) report of $2n = 18 + XY$ males in *L. notabilis*. Because Calabrese and Talerico's specimens of *L. notabilis* came from one of the same field populations that we studied, we doubt that the difference in results is explained by within-species variation, but reflects instead an error in interpretation on their part. We outline our reasons below.

Heteropteran chromosomes are unusual in a number of aspects of meiotic behavior. Most important for the present study is the behavior of the sex chromosomes (see White, 1973: 620; Ueshima, 1979: 4-9). In males of most families, if a Y is present, then the X and Y do not form a bivalent at first metaphase. As well, the first division is equational for the sex chromosomes. That is, the X and Y do not migrate to opposite poles (pre-reduction), but instead the two chromatids of the X separate and migrate to opposite poles, as do those of the Y if a Y is present (post-reductional sex chromosomes). Because each sex chromosome splits at first anaphase, each appears rather like an autosomal bivalent at first metaphase. It may thus be difficult to tell if a Y is present or if there is only an additional autosomal bivalent. If a male first metaphase has m "bivalents," then, the specimen may have either $2(m - 2)$ autosomes + XY or $2(m - 1)$ autosomes + X. If positional information is not available (Ueshima, 1979: 4-7), the only clear way to distinguish between these hypotheses from first metaphase cells is by close examination of each "bivalent"; if two of them are clearly 2-parted, and the rest are 4-parted, then the specimen probably has an X and Y; if only one element is 2-parted, then the specimen probably has only an X.

Calabrese and Talerico's published (1982: Fig. 5, 1984: Fig. 5) photographs of first metaphases in the two species are not of sufficient resolution to reveal the structure of each element (cf. Fig. 3). They apparently based their conclusions solely on male first metaphase cells, but they do not state how they determined the sex chromosome system.

To be more certain about the chromosome complement, stages other than first metaphase should be studied. Following is a series of predictions about chromosome numbers and structure for various meiotic stages and mitosis, under two different hypotheses about *L. notabilis*.

Hypothesis 1: sex chromosomes post-reductional, $2n = 18 + XY$; X and Y not forming MI bivalent, and not forming MII pseudobivalent. Predictions: *Males*: 1, MI with 11 elements, 2 2-parted; 2, MII with 11 elements, 2 1-parted; 3, spermatogonial mitosis with 20 elements. *Females*: 4, oogonial mitosis with 20 elements.

Hypothesis 2: sex chromosomes post-reductional, $2n = 20 + X$. Predictions: *Males*: 1, MI with 11 elements, 1 2-parted; 2, MII with 11 elements, 1 1-parted; 3, spermatogonial mitosis with 21 elements. *Females*: 4, oogonial mitosis with 22 elements.

Our results for *L. notabilis* match the predictions for the second hypothesis, $2n = 20 + X$, exactly (Table 1). Note as well that the equal MI and MII counts indicate that the X chromosomes are not pre-reductional.

In some hybrid crosses, nearly 50% of the eggs abort before hatching and F_1 hybrid females from either reciprocal cross are extremely rare or absent (Spence, unpublished). We suggest that rareness of female F_1 's results from interference between X chromosomes originating from females of both *L. dissortis* and *L. notabilis*. However, the more or less normal meiotic behavior observed in hybrid males does not prohibit production of fertile sperm; this conclusion is in accord with results of a study of gene flow between these species using electrophoretic techniques (Spence and Sperling, unpublished).

Although we do not claim that an XO sex chromosome system is necessarily universal among the Gerridae, we hold that present evidence for XY systems is inconclusive. Calabrese and Talerico (1982, 1984) reported presence of Y chromosomes in males of several gerrid species but we find their evidence about *Limnporus* unconvincing for the general reasons provided above. Also, for several additional species, their conclusions are at odds with our preliminary cytological observations. The only other report of Y chromosomes in gerrids known to us is for *G. paladum insularis* by Takenouchi and Muramoto (1968). However, evidence provided by their sketches of spermatocytes is equivocal with respect to the set of predictions that we state above. Their primary evidence is existence of two heteropycnotic bodies in pachytene cells of male meiotic prophase. In this connection, we note that Poisson (1936) reported precocious division of the X chromosome in some individuals of *G. lacustris* and *G. najas*. Such chromosome behavior is also consistent with the description given by Takenouchi and Muramoto (1968), and provides an alternative explanation for the two heteropycnotic bodies illustrated in their Fig. 30. Furthermore, it is not clear from the text that their results are based upon study of more than a single male. The interpretation for *G. paladum* is further clouded because drawings provided by Wilke (1913) suggest an XO system in another subspecies (*G. paladum paladum*). Study of the sex chromosome system was not a specific objective of Wilke's paper and the evidence provided about this point is weak.

To resolve discrepancies like that noted for *G. paladum* above and to promote better understanding of the evolution of chromosome systems in semi-aquatic bugs, future cytogenetic work must be presented with clear statements about how sex chromosome systems were determined. Also, labelled photographs of chromosomes should be provided that are adequate to allow readers to evaluate the interpretations offered.

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A REMARKABLE NEW AFRICAN AMISEGINE WASP
(HYMENOPTERA: CHRYSIDIDAE: AMISEGINAE)

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Abstract.—*Anachrysis paradoxa*, new genus and species, is described from Transvaal, South Africa and Botswana. Its affinities are with New World genera of Amiseginae rather than with other Ethiopian genera. It is hypothesized that *paradoxa* is a relict of a more ancient primitive amisegine fauna.

The discovery of a primitive wasp in a zoogeographic area where all previously known genera are extremely specialized is extraordinary. The new African amisegine described here is primitive in being fully winged in both sexes with a basically unmodified mesosomal structure. The five previously known African genera are highly modified creatures with a greatly altered mesosoma, flightless in both sexes, tiny wings, if present at all, concealed beneath the laterally expanded scutum.

Hosts are unknown for any African Amiseginae, but all females have sharp piercing mandibles, characteristic of the entire subfamily. These are adapted for penetration of the tough shell of the host eggs, first to feed on some of the fluid contents and then to oviposit therein. I listed the known hosts of nine Nearctic, Neotropical and Australian species (1983a: 8, table 1); all are walking sticks (Phasmatodea). I presume that the African species also parasitize eggs of Phasmatodea because of the uniform shape of the female mandibles.

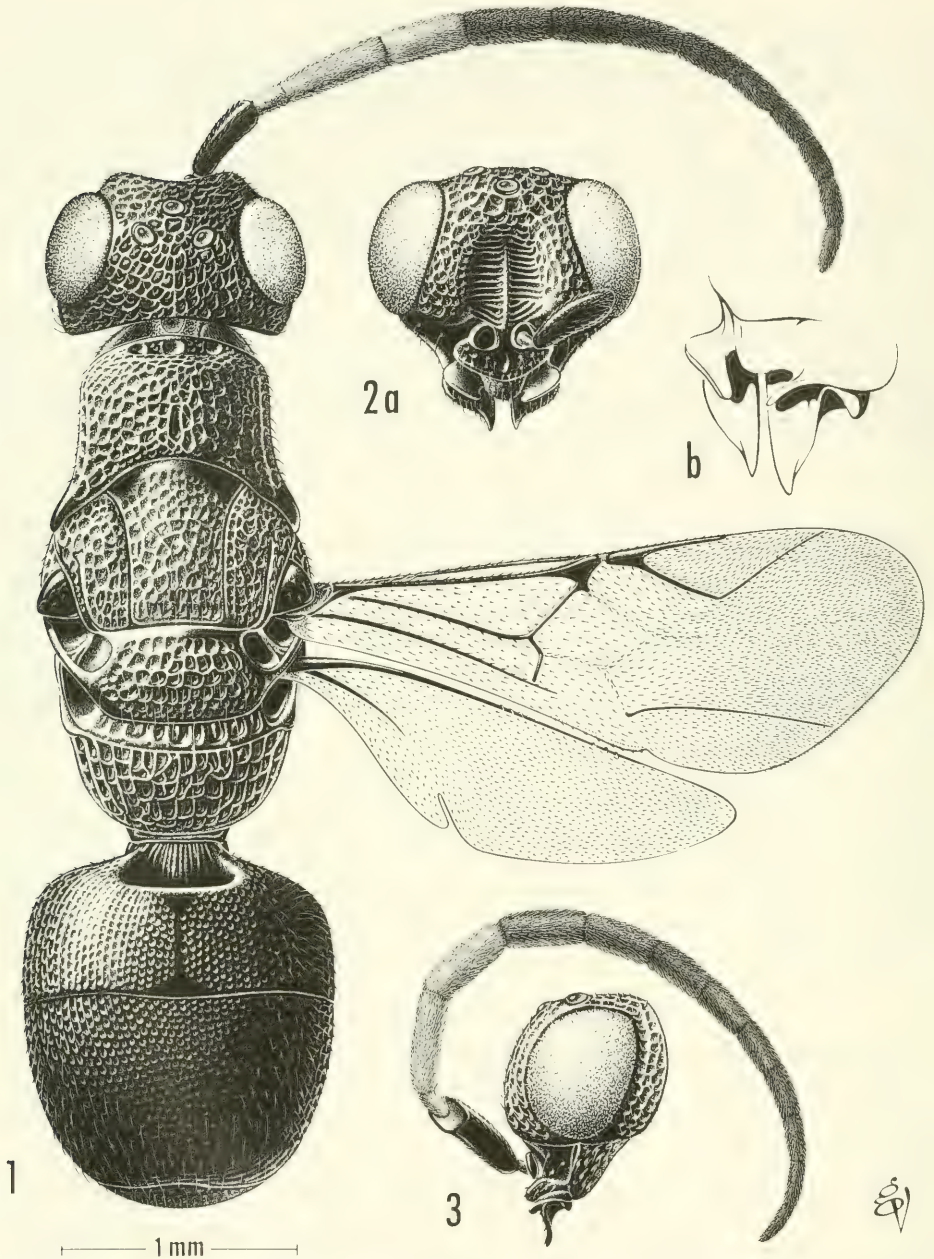
Anachrysis Krombein, NEW GENUS

Type-species.—*Anachrysis paradoxa* Krombein, by present designation.

Etymology.—The derivation is from the Greek *an*, not, and *Chrysis* Linnaeus, in allusion to its striking resemblance to many members of the Chrysidinae. The gender is feminine.

Diagnosis.—Moderately large, relatively slender, coarsely sculptured, fully winged Amiseginae with metallic blue integument.

Male.—Head in frontal view (Fig. 2a) about as high as wide, sides converging below; eyes moderately bulging, clothed with short, rather sparse microtrichiae, height 0.6 times distance from apex of clypeus to top of head; mandible large, flattened toward apex, dentate at tip; clypeal base raised into a low broad triangle, apical section depressed and thin, medially punctate, laterally smooth with edge reflexed outward into a colorless lamella (Fig. 2b), margin narrowly emarginate between the median and lateral areas; scapal basin moderately deep, margins not ridged; head unusually long behind eyes; occipital carina absent, but posterior and lateral margins of head angled abruptly to posterior surface; head in lateral



Figs. 1-3. *Anachrysis paradoxa*. 1, Dorsal aspect, left antenna and wings, and legs not shown. 2a, Head, frontal view, most of antennae not shown. 2b, Clypeus and mandibles, oblique frontolateral view, enlarged. 3, Head, lateral aspect.

view (Fig. 3); malar space with an oblique groove from lower eye orbit toward posterior mandibular condyle, 0.46 times eye height; gena abruptly widened behind lower third of eye; head posteriorly concave above hypostoma, carina of latter weak; antenna 13-segmented, elongate, scape three-fourths as long as pedicel

and first flagellar segment combined, flagellum with short dense suberect setae, segments twice or more as long as wide, tyli lacking.

Thorax in dorsal view (Fig. 1); pronotum long, 0.8 times length of scutum, disk lacking anterior and lateral carinae, depressed anteriorly and with three small deep pits, a short deep median groove near posterior margin, lobes not extending to tegulae; scutum with notauli complete, curved outwardly on basal third, converging posteriorly, parapsidal furrow on posterior half straight; scutellum 0.6 times as long as scutum; metanotum narrow, about a fourth as long as scutellum; mesopleural disk carinate anteriorly and with shallow furrow from a short distance below wing base running obliquely downward to edge of sclerite; propodeum rounded posteriorly, without posterolateral angles; forewing with radial vein extending about as far toward wing apex as costa, continuing to wing margin at an angle as a dark streak, basal vein with a small stub representing remnant of cubital vein, two discoidal cells delimited by wing creases, subdiscoidal vein a dark streak; hind wing with three hamuli about two-thirds from wing base; mid coxae slightly separated; tibial spurs 1-2-2; tarsi with short suberect bristles beneath; tarsal claw with small erect subbasal tooth.

Abdomen presumably with four normally exposed segments, but fourth tergum retracted in unique type, five visible sterna; apical margin of both second tergum and sternum with shallow median emargination.

Female.—Head as in male except mandible stout at base, tapering gradually to a slender acute apex, clypeal margin evenly rounded, without reflexed lamella laterally, and antenna 13-segmented, short and stout, scape as long as pedicel and first flagellar segment combined, the latter 0.9 times as long as 2-4 combined, segments 3-11 short, mostly as broad as long, flattened beneath and clothed with dense sensilla of several types (see Krombein, 1983a: 13, Figs. 39-45).

Thorax and appendages as in male except pronotum near posterior margin with a vague transverse carina on each side of the short median groove.

Abdomen with four exposed segments, ovipositor exerted, apical margin of second tergum convex, that of second sternum with shallow median emargination.

Anachrysis paradoxa Krombein, NEW SPECIES

The species is known from a male from Langjan Nature Reserve, Transvaal, South Africa, and four females from Farmers Brigade, Serowe, Botswana, about 250 km WNW of the Langjan area.

All wasps were taken in Malaise traps in open savanna. The male was collected in a vegetation type known generally in South Africa as sandveld. The kind of flora occurring at Langjan was described more precisely by Acocks (1975: 34-35, Fig. 22) as arid sweet bushveld, type b, *Grewia flava* veld. The average annual rainfall in bushveld ranges from 500 to 750 mm. C. D. Eardley wrote that the common trees in Langjan are *Grewia* spp., *Combretum apiculatum* Sonder, *Acacia* spp. and *Dichrostachys cinerea* Wight and Arnott. Several Malaise traps were operated in different areas of the Reserve, so there is no information on the specific tree which might have hosted the stick insect from whose egg the wasp emerged. The soil is very sandy in the Reserve.

The females were collected in traps on soil with interspersed stones or gravel, the dominant trees being *A. nigrescens* Oliver and *C. apiculatum* with *Grewia* sp. and *D. cinerea* growing nearby. P. Forchhammer stated that the altitude around

Serowe is about 1500 m and that the vegetation was classified by Weare and Yalala (1971) as *Acacia nigrescens/Combretum apiculatum* tree savanna. He also mentioned that the rainfall around Serowe during periods of insect activity ranged from 214 to 721 mm in the seasons 1977–78 through 1983–84 (no record for 1981–82). The pristine condition of all females suggests that they had emerged only a short time before their capture, and the scattered collecting dates indicate that breeding may occur over an extended period in arid semitropical to tropical regions.

Etymology.—The name is from the Latin *paradoxus*, contrary to all expectation.

Diagnosis.—Characters of genus and as follows.

Male.—Length 4.5 mm, forewing 2.6 mm. Integument metallic blue, pedicel and base of flagellum light brown, apical segments and tarsi darker brown; wings hyaline, veins dark. Vestiture silvery, sparse, short and erect.

Head (Figs. 1–3): Basal raised area of clypeus with a few scattered small punctures; scapal basin closely transversely carinate, a weak narrow ridge medially; head laterad of scapal basin and on top closely foveolate; gena 0.46 times eye height; vertex with median carina; antenna elongate; flagellum decreasing gradually in width toward apex, first segment a third as wide as long, relative lengths of segments as 37:30:24:24:22:22:19:16:15:13:18.

Thorax with slightly larger foveolations than head; propodeum with somewhat larger irregular reticulations, more strongly so dorsally and posteriorly than laterally.

Disk of first tergum with small close punctures, a narrow median area smooth; second tergum with small close punctures, those laterally arranged in longitudinal rows, posteriorly in middle with sparse punctures, posterolaterally with a few weak oblique carinae; exposed part of third tergum with scattered tiny punctures; second sternum with small subcontiguous punctures except narrowly along midline and posteriorly.

Female.—Length 4.9 mm, forewing 3.0 mm. Coloration and vestiture as in male except flagellum black, mandible light red, tarsi brown.

Head as in species description of male except antenna shorter, flagellum stout, relative lengths of segments as 16:6:7:6:6:6:6:5:5:7, segment 1 three times as long as greatest width, segments 2–7 as broad as long, segments 8–10 somewhat longer than wide, and 11 twice its width.

Thorax and abdomen as in specific description of male.

Holotype: ♂, SOUTH AFRICA, TVL (Transvaal), Langjan Nature Reserve, 22:52 S, 29:14 E, 10–20 January 1980, G. L. Prinsloo, C. Kok, C. D. Eardley, P. Smith, in Malaise trap; (National Collection of Insects, Pretoria, South Africa). **Allotype:** ♀, BOTSWANA, Serowe, (22:25 S, 26:44 E), VI-1985, P. Forchhammer, in Malaise trap; (British Museum (Natural History)). **Paratypes:** 3 ♀, same locality and collector as allotype but 26 May, 11 June and 2–6 August 1983, presumably all taken in Malaise trap but not so labeled.

Remarks.—I believe that the male and females represent opposite sexes of the same species. Color and integumental sculpture are remarkably concordant. Such notable differences as occur in the shape of the mandibles, clypeus, antennae and number of normally exposed abdominal segments are consistent with the sexual dimorphism found in many other Amiseginae. The one differentiating character not likely to be sex-linked is the presence in only the female of a vaguely defined

transverse carina near the posterior margin of the pronotum. Although the holo- and allotype localities are some 250 km distant, it should be noted that each is open savannah with many of the same trees and grasses.

The paratypes are very similar to the type in all details except that the female collected in August has red tibiae and tarsi.

DISCUSSION

The Amiseginae are essentially a pantropical group with a Gondwana-type distribution (Krombein, 1983a, map on p. 6). Its surprising absence from Madagascar may reflect failure to collect in and on leaf litter, the specialized habitat where most amisegines are to be found. Only two fossil Amiseginae are known, *Protamisega* Evans from Siberian amber of Cretaceous age and a new genus (Krombein, in prep.) from Baltic amber of Eocene age, both areas with a warm climate during those eras.

Thirty years ago I reviewed the available material of recent Amiseginae (Krombein, 1957) and recognized three distinct groupings based primarily upon thoracic modifications. As modified by additional material in subsequent papers (1960, 1983a, b, 1984) these divisions may be characterized as follows. The primitive American Series has a narrow metanotum (absent in *Microsega* Krombein) that is noticeably shorter than the scutellum, is fully winged in both sexes except *Microsega*, and has the propodeal dorsum rounded or dentate posterolaterally. The more specialized Australasian Series has a metanotum as long as or longer than the scutellum, fully winged males, fully winged or brachypterous flightless females, and the propodeal dorsum angulate or dentate posterolaterally. The highly specialized African Series has an occipital carina, lacks a median pronotal groove, is flightless in both sexes, has the scutum expanded laterally so that tiny wings and tegulae, if present at all, are concealed in dorsal view, an enlarged metanotum covering almost the entire dorsal area of the mesosoma posteriorly, and the propodeum virtually absent dorsally and sloping gradually downward or abruptly declivous posteriorly, the dorsal posterolateral thoracic angles not produced.

The unexpected, remarkable new African taxon described above is more similar to the American genera than it is to any of the previously known African genera. It has a narrow metanotum, is fully winged and the propodeal dorsum is rounded posterolaterally.

The Neotropical *Duckeia* Costa Lima is similar to *Anachrysis* in such characters as the longer malar space (ca. 0.6 times eye height), well-developed, transversely carinate scapal basin, flagellar segments in female broader, flattened and densely covered beneath with numerous sensilla, the lack of an occipital carina, a median pronotal groove, the propodeal dorsum rounded posterolaterally and the metallic blue, coarsely sculptured integument. (This particular integument occurs elsewhere in the Amiseginae only in the Oriental *Rohweria* Fouts.) *Duckeia* differs from *Anachrysis* in its stocky build, in having the darkened streak almost closing the marginal cell curving evenly toward the wing margin rather than being at an angle to the radial vein, in the strong flange posteriorly on the gena and in having the base of the second abdominal sternum raised into a median projection.

Three other New World genera lack an occipital carina and have the propodeal dorsum rounded posterolaterally. *Amisega* Cameron and its probable synonym, *Mesitiopterus* Ashmead, have a short malar space less than 0.2 times the eye

height, comparatively longer flagellar segments in the females, not so flattened beneath and furnished with fewer sensilla, lack a median pronotal groove and a marginal cell shaped as in *Duckeia*. *Microsega* Krombein is highly aberrant and the most specialized of the New World genera; both sexes lack a metanotum and have the wings reduced to pads no larger than the tegulae.

Adelphe Mocsary and *Nesogyne* Krombein, formerly placed in the Adelphinae, are probably the least closely related of the New World genera. They have a poorly developed scapal basin, an occipital carina and the propodeal dorsum is dentate or spinose posterolaterally.

Anachrysis is probably to be regarded as a relict in the African region, and not directly ancestral to the rest of that fauna which is likely to have evolved from the Australasian Series. Unquestionably its affinities are with the New World genera. Inevitably one wonders whether other relict genera may not be found elsewhere in the Old World. My collecting in Sri Lanka (1983a) was a convincing demonstration that there must be a large uncollected amisegine fauna in the Oriental Region.

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AGABUS (COLEOPTERA: DYTISCIDAE) LARVAE OF SOUTHEASTERN UNITED STATES

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Abstract.—Six newly associated larvae of the genus *Agabus*, *A. punctatus*, *A. aeruginosus*, *A. stagninus*, *A. erythropterus*, *A. seriatus*, and *A. obtusatus*, are described and a key to the known larval forms from southeastern United States is presented. Southeastern species of *Agabus* for which larvae are unassociated are briefly discussed.

The genus *Agabus* Leach is probably the largest and most complex non-hydroporine dytiscid genus in North America. Its distribution is primarily northern, however, and only 16 species occur in the southeastern states (Virginia, North and South Carolina, Georgia, Florida, Alabama, Mississippi, and Tennessee). Southeastern adults may be keyed with Michael and Matta (1977) or Brigham (1982). Michael and Matta omit *Agabus bifarius* (Kirby) and Brigham omits several principally northern species that are occasionally found in the Virginia and West Virginia mountains.

Larval *Agabus* are found in most vernal pools and in backwater areas of streams. They are fierce predators and while usually not the top predator in a system they are frequently the most numerous of the larger invertebrate predators. They frequently coexist with small fish and amphibian larvae and have been observed feeding on fish larvae.

The larvae of 10 North American *Agabus* have been described (James, 1969; Watts, 1970; Barman, 1972; Hilsenhoff, 1974) and 5 of these, *Agabus ambiguus* Say, *Agabus bifarius*, *Agabus confusus* (Blatchley), *Agabus disintegratus* Crotch, and *Agabus semivittatus* LeConte, occur in the southeast. In this paper six newly associated larvae are described and a key to the 11 known larval forms from southeastern United States is presented.

Five southeastern species remain to be associated. Three of these, *Agabus anthracinus* Mannerheim, *Agabus planatus* Sharp, and *Agabus taeniolatus* (Harris), are primarily northern in distribution and are rarely collected in the southeast. *Agabus gagates* Aubé and *Agabus johannis* Fall are common in the southeast and larval stages should be frequently encountered. Tentatively associated but unreared specimens lead me to believe that both species will key to couplet 7.

METHODS

A method for rearing hydroporine larvae was presented by Matta and Peterson (1984). This method has worked equally well with larger larvae and was used in rearing the larvae described here.

Measurements were made with an ocular micrometer in a Wild M8 microscope at 10× (body length to the nearest 0.1 mm) or 50× (other measurements to the nearest 0.02 mm). When ratios are given for segmented appendages, the basal segment is given first and the value given in the ratio is the length in millimeters.

Abbreviations used in the descriptions for the placement of spines on the legs are: AV = anteroventral, PV = posteroventral, and D = dorsal, as proposed by Wolfe and Roughley (1984).

DIAGNOSIS FOR THIRD INSTAR LARVAE OF SOUTHEASTERN *AGABUS*

Color of integument yellowish white. Dorsal sclerites of abdomen peppered with black spots that mark the points of insertion of setae; spots densest on segments 6–8. Venter and legs yellowish white, legs with dark markings at base of coxae.

Head subquadrate, posterior fifth severely constricted, without a cervical ridge. Stem of epicranial suture more than half as long as head. Six ocelli located in an upright oval patch at anterior third of head. Antenna 4-segmented, inserted just in front of the ocelli. Maxillary stipe about 3 times as long as wide, with a short fingerlike projection on the inner apical angle.

Thorax with mesothoracic spiracles on membranous area, without pro- and metathoracic spiracles. Fore- and midlegs subequal in length; hindlegs longer, almost reaching last abdominal segment.

Abdomen with segments 7 and 8 completely sclerotized ventrally; segments 1–6 membranous ventrally; with spiracles on mesolateral margins of sclerotized areas of terga 1–6 and ventrolaterally on segment 7. Black setae relatively short and inconspicuous on anterior segments, becoming longer and more numerous on posterior segments.

Agabus punctatus Melsheimer

Third instar larvae.—Length 10.0 mm (not including cerci). Dorsal sclerites with a median and 2 sublateral brown stripes that become confluent and diffuse on abdominal segments 6–8; stripes with 1 or 2 variably placed light spots on thoracic segments and abdominal segments 1–5. Head with three temporal spines present laterally in an anteriorly descending line just anterior to the cervical constriction. Ocelli located on end of each lateral stripe. Antennal ratio 0.25:0.20:0.20:0.05; palpal ratio 0.20:0.25:0.20. Labium short, about 3 times as wide as long; palpal ratio 0.25:0.20. Thorax with no precoxal sclerite present. Swimming hairs present on all tarsi and tibia but fewer present on front legs. Chaetotaxy: protarsi, AV-0, PV-0, D-0; protibia, AV-2, PV-0, D-0; mesotarsi, AV-0, PV-0, D-0; mesotibia, AV-6, PV-1, D-0; metatarsi, AV-6, PV-0, D-3 to 4; metatibia, AV-7 to 9, PV-1, D-3 to 4. Margins of sclerotized areas of terga 1–6 and ventrolaterally on segment 7. Cerci about equal in length to eighth abdominal segment; 2-segmented, second short and spikelike; first segment with 3 long setae on basal fifth and 4 long setae at apex.

Described from 27 larvae (5 reared) collected from open temporary pools in The Great Dismal Swamp, Virginia, April 9 to June 1.

Agabus aeruginosus Aubé

Third instar larva.—Length 10.0 mm (not including cerci). Dorsal sclerites with a median and 2 sublateral brown stripes that become confluent and diffuse on abdominal segments 6–8; stripes with 1 or 2 variably placed light spots on thoracic segments and abdominal segments 1–5. Head with 3 temporal spines present laterally in an anteriorly descending line just anterior to the cervical constriction. Ocelli located on end of each lateral stripe. Antennal ratio 0.25:0.20:0.20:0.05. Maxillary palpal ratio 0.20:0.25:0.20. Labial palpal ratio 0.25:0.20. Thorax with no precoxal sclerite present. Swimming hairs present on all tarsi and tibia but fewer present on front legs. Chaetotaxy: protarsi, AV-0, PV-0, D-0; protibia, AV-2, PV-0, D-0; mesotarsi, AV-0, PV-0, D-0; mesotibia, AV-3 to 4, PV-1, D-2 to 3; metatarsi, AV-5 to 6, PV-0, D-3 to 4; metatibia, AV-6 to 7, PV-1, D-4. Cerci about equal in length to eighth abdominal segment; 2-segmented, second short and spikelike; first segment with 3 long setae on basal fifth and 4 long setae at apex.

Described from 6 larvae (1 reared) collected from open temporary pools in The Great Dismal Swamp, Virginia, February 13, March 14, and March 24.

Agabus stagninus Say

Third instar larva.—Length 11.2 mm (not including cerci). Dorsal sclerites brown, lighter laterally, with the posterior margins darker; light spots present on thoracic segments and abdominal segments 1–5. Prothorax with additional light spots on the disk. Head brown, mottled on posterior and posteriolateral margins; with a complex mottling on the anterior third which leaves a cruciform dark area medially. Head with four temporal spines present laterally in an anteriorly descending line just anterior to the cervical constriction. Antennal ratio 0.30:0.27:0.30:0.12. Maxillary palpal ratio 0.25:0.25:0.22. Labial palpal ratio 0.30:0.22. Prosternum with precoxal sclerite present. No swimming hairs present on tarsi and tibia. Chaetotaxy: protarsi, AV-0, PV-0, D-0; protibia, AV-0, PV-3, D-0; mesotarsi, AV-2, PV-0, D-0; mesotibia, AV-3, PV-1, D-0; metatarsi, AV-5, PV-0, D-0; metatibia, AV-5, PV-1, D-0. Cerci shorter than eighth abdominal segment, ratio 1.25:1.50; 2-segmented, second segment short and spikelike; first segment with 3 long setae on basal fourth and 4 long setae at apex.

Described from 10 larvae (reared). Larvae were collected from heavily shaded temporary pools in The Great Dismal Swamp, Virginia, March 11 to April 21. The pools were under loblolly pines and heavily littered with pine needles. Numerous isopods (*Asellus* sp.) and the larvae of *Laccornis difformis* (LeConte) (Coleoptera: Dytiscidae) were also collected from these pools.

Agabus erythropterus Say

Third instar larva.—Length 11.5 mm (not including cerci). Dorsal sclerites light brown, lighter laterally; light spots present on thoracic segments and abdominal segments 1–5. Prothorax with additional light spots on the disk. Head light brown, mottled on posterior and posterolateral margins; with a complex mottling on the anterior third which leaves a cruciform dark area medially. Six temporal spines present laterally in an anteriorly descending line just anterior to the cervical constriction. Antennal ratio 0.20:0.20:0.25:0.12. Maxillary palpal ratio 0.20:0.20:

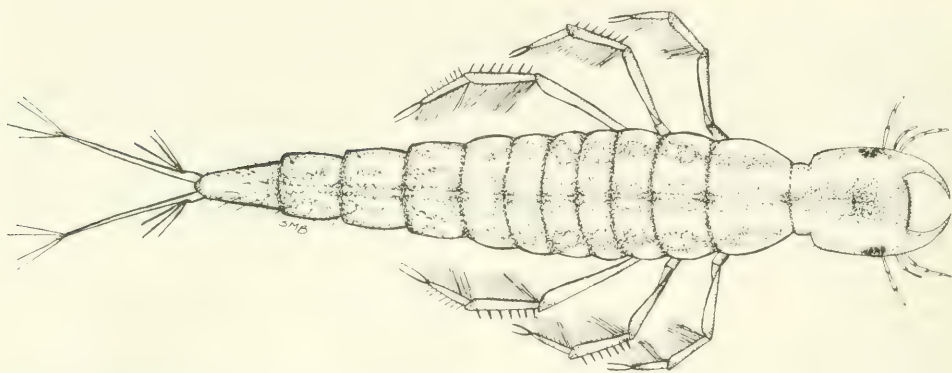


Fig. 1. *Agabus punctatus*, habitus, dorsal view.

0.12. Labial palpal ratio 0.20:0.12. Hindleg almost reaching sixth abdominal segment; no swimming hairs present on tarsus and tibia. Chaetotaxy: protarsi, AV-0, PV-0, D-0; protibia, AV-0, PV-2 to 3, D-0; mesotarsi, AV-2, PV-2, D-0; mesotibia, AV-1, PV-1, D-0; metatarsi, AV-3 or 4, PV-2, D-0; metatibia, AV-3 or 4, PV-1, D-0. Cerci longer than eighth abdominal segment, ratio 2.00:1.60; 2-segmented, second segment short and spikelike; first segment with 3 setae on basal fourth, reaching to the midpoint of cerci, and 4 long setae at apex.

Described from 4 larvae (1 reared). Larvae were collected from grassy areas of an open marshy pool in Pendleton Co., West Virginia, July 21, 1983.

Agabus seriatus Say

Third instar larva.—Length 10.5 mm (not including cerci). Dorsal sclerites brown; light spots present on thoracic segments and abdominal segments 1–5. Prothorax with additional light spots on the disk. Head light brown, mottled on posterior and posteriolateral margins; with a complex mottling on the anterior third which leaves a cruciform dark area medially. Five temporal spines present laterally in an anteriorly descending line just anterior to the cervical constriction. Antennal ratio 0.35:0.32:0.32:0.16. Maxillary palpal ratio 0.35:0.35:0.30. Labial palpal ratio 0.50:0.30. Prosternum with precoxal sclerite present. No swimming hairs present on tarsi and tibia. Chaetotaxy: protarsi, AV-3, PV-3, D-1; protibia, AV-4, PV-0, D-1; mesotarsi, AV-3, PV-3, D-2; mesotibia, AV-3, PV-3, D-2; metatarsi, AV-5 or 6, PV-3 or 4, D-3 or 4; metatibia, AV-5 or 6, PV-4, D-3 or 4. Cerci longer than eighth abdominal segment, ratio 1.50:1.20; cerci 2-segmented, second segment short and spikelike; first segment with 3 long setae on basal fourth, reaching beyond the midpoint to cerci, and 4 long setae at apex.

Described from 6 larvae (1 reared). Larvae were collected from a weed- and algae-choked stream, Seneca, New York, July 26, 1982. Many adult *A. seriatus* have been collected in Virginia and West Virginia, but larvae have not been collected in the southeast.

Agabus obtusatus Say

Third instar larvae.—Length 10.5 mm (not including cerci). Dorsal sclerites brown; light spots present on thoracic segments and abdominal segments 1–5.



Fig. 2. a, Midleg of *Agabus punctatus*, anterolateral surface. b, Hindleg of *Agabus disintegratus*, posterolateral surface.

Prothorax with additional light spots on the disk. Head brown, mottled on posterior and posteriolateral margins; with a complex mottling on the anterior third which leaves a cruciform dark area medially. Seven temporal spines present laterally in an anteriorly descending line just anterior to the cervical constriction. Antennal ratio 0.25:0.25:0.25:0.12. Maxillary palpal ratio 0.25:0.20:0.20. Labial palpal ratio 0.35:0.25. Prosternum with precoxal sclerite present. No swimming hairs present on tarsi and tibia. Chaetotaxy: protarsi, AV-0, PV-0, D-0; protibia, AV-3, PV-1, D-0; mesotarsi, AV-0, PV-0, D-0; mesotibia, AV-2, PV-0 to 1, D-0; metatarsi, AV-2, PV-1, D-1 to 2; metatibia, AV-4, PV-2, D-1 to 2. Cerci shorter than eighth abdominal segment, ratio 1.80:1.40; 2-segmented, second segment short and spikelike; first segment with 3 setae on basal fourth and 4 setae at apex. Described from 2 larvae (1 reared). Larvae were collected from an alpine meadow, Dolly Sods, West Virginia, 5 May 1974 and from a marshy stream margin, Greenbrier Co., West Virginia, June 18, 1983.

KEY TO THE KNOWN *AGABUS* LARVAE OF SOUTHEASTERN UNITED STATES

- 1. Cerci $\frac{1}{3}$ length of last abdominal segment. *bifarius*
- Cerci $\frac{1}{2}$ length of last abdominal segment or longer 2
- 2. Cerci with many secondary hairs in addition to the 7 primary hairs *confusus*
- Cerci with only 3 basal and 4 apical primary hairs 3
- 3. Long swimming hairs present on all legs 4
- Swimming hairs absent from all legs although long spines may be present 5
- 4. Midtibia with 3-4 anteroventral, 1 posteroventral and 2-3 dorsal spines *aeruginosus*
- Midtibia with 6-7 anteroventral and 1 posteroventral spines, without dorsal spines (Fig. 2a) *punctatus*
- 5. Cerci longer than twice length of last abdominal segment; mid- and hindtibia with 3-5 long dorsal setae (Fig. 2b) that are longer than twice the width of the tibia *disintegratus*
- Cerci less than twice length of last abdominal segment; if dorsal setae present then they are shorter than tibial width, and usually fewer than 3 6
- 6. Cerci less than or equal to length of last abdominal segment 7
- Cerci distinctly longer than last abdominal segment 8
- 7. Abdominal segment 6 completely sclerotized; cerci with setae on basal third; piedmont and mountain species (Based on Barman, 1972. I have not seen the larva of this species.) *ambiguus*

- Abdominal segment 6 not completely sclerotized; cerci with 3 setae on basal third; coastal plain species *stagninus*
- 8. Hindtibia and hindtarsus with dorsal setae 9
- Hindtibia and hindtarsus without dorsal setae 10
- 9. Head with distinct cervical ridge; hindtarsus with 2 anteroventral spines *obtusatus*
- Head without cervical ridge; hindtarsus with 5–6 anteroventral spines *seriatus*
- 10. Head with distinct cervical ridge *semivittatus*
- Head without cervical ridge *erythropterus*

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**BIOLOGY OF *SUMITROSIS ROSEA*
(COLEOPTERA: CHRYSOMELIDAE), A LEAFMINER OF
BLACK LOCUST, *ROBINIA PSEUDOACACIA* (LEGUMINOSAE)**

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Abstract.—Data are presented on life history of the chrysomelid *Sumitrosis rosea* (Weber), a univoltine leafminer of black locust, *Robinia pseudoacacia* L. (Leguminosae). Its distribution, host range, and habits are compared and contrasted with those of the well-known locust leafminer, *Odontota dorsalis* (Thunberg), a co-occurring member of the same tribe (Chalepini). Although the scorched appearance and premature defoliation of black locust can be attributed to feeding by *O. dorsalis*, the often overlooked *S. rosea* may intensify the damage.

The genus *Sumitrosis* Butte belongs to the chrysomelid subfamily Hispinae and contains 55 mainly Neotropical species. Only six are known from America north of Mexico, with *S. inaequalis* (Weber) and *S. rosea* (Weber) the most common and widely distributed. Both hispines, though varying in color and sometimes occurring in the same habitat (Ruesink, 1984; McPherson, 1985), are readily separable by characters given in Butte's (1969) key: pale yellow antennae and angulate posterolateral elytral angles in *rosea*, contrasted with piceous antennae and rounded elytral angles in *inaequalis*. Their principal host plants, however, have been misassigned. Wilcox (1954) reported *S. inaequalis* as a legume feeder and *S. rosea* as associated with composites. Following Wilcox (1954), Balsbaugh and Hays (1972) stated that larvae of *inaequalis* mine leaves of plants in the Leguminosae. The actual host preferences of the two species are just the reverse, as Ford and Cavey (1985) pointed out; they suspected that Butte's (1969) report of *Chenopodium album* L. (Chenopodiaceae) as a larval host was based on a misidentification of the plant. The host range is also said to include Urticaceae, especially wood nettle, *Laportea canadensis* (L.) Wedd. (Hicks, 1965; Riley and Enns, 1979; McPherson, 1985), and we also have observed a hispine species developing on this plant. Although the forms reared from various legumes and wood nettle may indeed be conspecific, it is unusual for a North American hispine to mine the leaves of plants in such distantly related families.

On black locust, *Robinia pseudoacacia* L. (Leguminosae), mines of *S. rosea* often co-exist with those of another hispine, *Odontota dorsalis* (Thunberg), the locust leafminer. In contrast to this well-studied tree pest (e.g. Chittenden, 1902; Dominick, 1938; Haviland, 1943; Fritz, 1983; Kirkendall, 1984), the habits of *S. rosea* are poorly known. It was not mentioned in Chambers' (1880) account of insects occurring on black locust in Kentucky, Schwarz' (1891) list of Coleoptera

associated with *R. pseudoacacia* in the Washington, D.C., area, or in Weaver and Dorsey's (1965) study of the natural enemies of leafmining insects on this tree in West Virginia. When this hispine has been treated, most authors merely have noted its collection from black locust. Butte (1969) gave a list of synonyms for *S. rosea* but did not record misidentifications appearing in certain faunal lists and in the economic literature. Thus, some of the few papers containing notes on *S. rosea* have been overlooked owing to the confusing usage of the name *nervosus*.

Baliosus nervosus (Panzer) apparently is the correct name for the basswood leafminer (see Uhmman, 1957; Ruesink, 1984). This name assignment, however, has not generally been followed by North American workers. *Baliosus nervosus* of authors has been variously applied. Chittenden's (1902) observations refer to *S. inaequalis* and *S. rosea*, with his record of a "pale variety or race" on *Robinia neomexicana* A. Gray in Arizona referring to *rosea* [see Butte (1969: 17); Needham et al. (1928) incorrectly cited this tree as a host of *inaequalis*]. Based on host data cited (composites or legumes), other economic workers have used *nervosa* for *inaequalis* (e.g. Beutenmüller, 1890; Ouellet, 1919) or for *rosea*. Observations in the following papers apparently refer to adults of *rosea* (cited in *Chalepus* or *Odontota*): West Virginia: "quite plentiful" or "very common" on black locust, feeding on upper surface of leaves (Hopkins, 1891, 1893); Ohio: common on locust foliage (Cotton, 1906) and occasionally "fairly abundant"; sometimes found on dogwood (Houser, 1918); New Jersey: common on locust throughout state (Smith, 1910); New York: occurring with *O. dorsalis* on locust on Long Island, termed the "rosy hispa" (Felt, 1912); and Kentucky: common on locust (Garman, 1916).

With the exception of Chittenden (1902), who reared *S. rosea* from mines on black locust leaves, early writers did not provide data on immature stages. This is hardly surprising because its mines are indistinguishable from those of the locust leafminer, whose mines usually "swamp" those of the less numerous *S. rosea*. We note that one of the six undetermined larval forms that Hopkins (1891) observed in blisterlike mines on black locust leaflets in West Virginia may have been that of *S. rosea*. But larvae were unknown when Butte (1969) revised the genus, though the mature (third-stage) larva has now been described and illustrated (Ford and Cavey, 1985). The inconspicuous, singly deposited eggs have not been described and perhaps have gone unnoticed.

Recent authors have added several legumes as larval hosts, e.g. *Desmodium* sp. and *Lespedeza intermedia* (S. Watts.) Britt. (Ford and Cavey, 1985) and measured adult foliage consumption and area occupied by mines on soybean, *Glycine max* (L.) Merrill (Buntin and Pedigo, 1982; cited as *Baliosus nervosus*, see Ruesink, 1984). The seasonal history and habits of *S. rosea* have not been elucidated. Here, we summarize our observations on its seasonal history and host plants in Pennsylvania and its behavior on black locust in the greenhouse. We also observed *Odontota dorsalis* in the field and greenhouse. The distribution, host range, habits, and natural enemies of these two hispines are compared and contrasted.

MATERIALS AND METHODS

During 1982–85, black locusts in the Harrisburg, Pennsylvania, area were examined every 1–3 days once leaf flush had begun (late April–early May) to detect emergence of overwintered adults of *S. rosea* and *O. dorsalis*. Once beetles had

begun to emerge, two small groves of shrubby trees were monitored for 15–20 minutes at 7- to 10-day intervals to record the relative numbers of adults present and to make behavioral observations. After oviposition began, the life stages observed on black locust leaflets were noted, though actual numbers of eggs, larvae, and pupae were not recorded. The periodic censuses continued through August to determine whether either species produced a second generation. In December 1985, leaf litter taken beneath black locust was examined for the presence of overwintering beetles. Supplemental field observations were made on populations of *S. rosea* occurring on locust and other hosts in southcentral Pennsylvania; Ithaca, New York; and several localities in the southern Appalachians.

The laboratory rearings were carried out in a greenhouse under natural photoperiod. In 1984, overwintered adults of *S. rosea* were placed on 3 black locust saplings in a small cage at temperatures ranging from 22–33°C and relative humidity of 50–90%; locust leafminer adults were placed on black locust in an adjoining cage under similar conditions. The habits of both species were observed twice daily. In 1985, mating pairs of *S. rosea* were collected on 3 June and a pair placed on each of 14 black locust seedlings. Clear plastic (Mylar) cylinders covered at the top with nylon mesh were placed over the plants; the plants were then put in a small cage. Humidity inside the cylinders was not measured, but the condensation forming on the inner surface suggested it was higher than the 50–90% in the cage. Fecundity of each of 11 females was determined by examining seedlings twice daily for eggs and placing small, numbered adhesive disks adjacent to each egg. To determine stadia without disrupting the larvae, mines were illuminated from the underside with a handheld, concentrated light source (pen light). To verify our determination of larval instars, the roof of a mine was pulled back periodically with forceps to detect cast skins. Data on fecundity, longevity, incubation period, egg size, and first and second stadia are given as means $\pm$ SE.

BIOLOGY

Distribution and host plants.—*Sumitrosis rosea* is known from Ontario south to Florida and west to Manitoba, Kansas, and Arizona (Butte, 1969). Our collecting in eastern United States suggests that this hispine is common in the Mid-Atlantic region and southern Appalachians but infrequent and patchily distributed north of Pennsylvania where black locust, its principal host, is not native but widely naturalized (Li, 1963; Little, 1971). Butte (1968) gave a similar eastern range for *O. dorsalis*—Ontario to Georgia—but examined material only from as far west as Illinois. Records for the locust leafminer now are available for all states east of the Mississippi and from Arkansas, Louisiana, and Missouri (Cannon, 1970; USDA, 1977).

Adults of *S. rosea* have long been known to occur on black locust trees, and larvae have been reared from mines on locust leaflets (see introduction). Thus, the statement that no species of the genus is known to use a tree as a larval host (Ruesink, 1984) is incorrect. In addition to the other leguminous hosts noted, goldenchain, *Laburnum* sp., appears to serve as a host plant. In early September 1981 a population estimated at several hundred adults was observed on an isolated goldenchain tree in Northumberland Co., Pennsylvania. Adult feeding, so severe that nearly every leaflet showed injury, had rendered the tree unaesthetic in appearance. A few old eggs of *O. dorsalis* were present, but most empty mines were

probably those of *S. rosea*. At a nursery in the same county, adults were present on goldenchain trees during June and July.

Black locust is thought to represent the prime and original host of *O. dorsalis* (Chittenden, 1902). Locust leafminer also develops on false indigo, *Amorpha fruticosa* L. (Chittenden, 1902), and bristly locust, *Robinia hispida* L. (Ford and Cavey, 1985). The host range also includes several exotic legumes: soybean (Poos, 1940; McPherson and Ravlin, 1983); Japanese pagodatree, *Sophora japonica* L.; and goldenchain, *Laburnum × waterei* (Wheeler, 1980). A new host record is yellowwood, *Cladrastis lutea* L. We observed eggs, larvae, and adults on this leguminous tree in York Co., Pennsylvania and at Ithaca, New York.

Seasonal history and habits.—We collected an adult of *S. rosea* (and one of *O. dorsalis*) overwintering in locust leaves beneath host trees. In Virginia, locust leafminer adults are known to hibernate in thick masses of loosely matted leaves, the beetles clinging to lower leaf surfaces of oak, maple, and those of other deciduous tree species. Winter survival of *O. dorsalis* in three wire screen cages containing 50, 90, and 201 beetles ranged from 88–92% (Haviland, 1943). In the Harrisburg area we swept an overwintering *S. rosea* from weeds beneath black locust on 18 April, but adults did not appear on host trees until late April or early to mid-May, typically on small trees within 7–10 days of leaf flush and a few days to a week after the first locust leafminer adults were present. When disturbed on their host, adults quickly dropped to the ground, a behavior displayed by *O. dorsalis* (Hopkins, 1891) and *S. inaequalis* (Ouellet, 1919). After several days of warm weather, adults became more numerous on black locust and began to feed on the upper and lower surfaces of host foliage. The characteristic feeding posture, abdomen elevated 30–45° above the leaflet surface, is shown in Fig. 1; occasionally a beetle's abdomen was nearly perpendicular or parallel to the surface during feeding. *Sumitrosis rosea* fed by scraping the epidermis and sometimes cutting tiny holes in a leaflet. In the laboratory a beetle fed briefly on the stem of a locust sapling. We also observed an adult feeding on a leaflet of *Robinia hispida* but did not observe a general dispersal to nonhost plants. In Iowa, adults have been reported to feed on foliage of lima and field bean (Buntin and Pedigo, 1982). Locust leafminer adults fed similarly on black locust, though the elevated-abdomen posture was only rarely seen. They imparted a netted or skeletonized look to the foliage and usually made larger and more numerous holes in leaflets and used a wider range of plant species for adult feeding. *Odontota dorsalis* attacks various herbaceous and woody plants, sometimes injuring the foliage of apple and other fruit trees (Hopkins, 1896; Chittenden, 1897, 1902; Dominick, 1938; Haviland, 1943). We observed adults of both hispines feeding on black locust petals and collected adults in inflorescences where they may have been feeding on nectar and pollen. *Odontota dorsalis* is known to visit flowers of black locust (Lovell, 1915) and to exploit nectar in inflorescences of fly-poison, *Amianthium muscaetoxicum* (Walter) Gray, and is one of the main pollinators of this liliaceous plant (Travis, 1984).

In nature we first observed mating pairs of *S. rosea* from 3 days to 2 weeks after overwintered beetles appeared on host trees. Our earliest record of copulation was 7 May. There was no elaborate courtship ritual observed under laboratory conditions. The male approached a potential mate, then pounced on her dorsum.

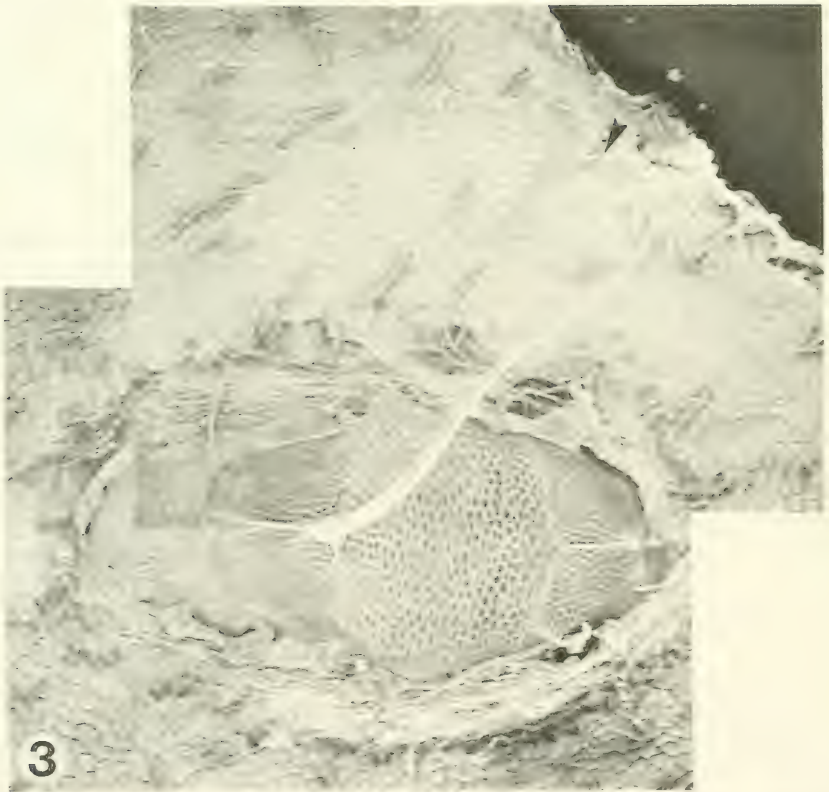


Fig. 1. Typical feeding posture of *Sumitrosis rosea* on black locust leaflets.

With the pair facing in the same direction, he quickly attempted intromission. In one pair, we observed a violent antennal quivering in both sexes, with the male mounted on the female prior to intromission. Antennal quivering may be part of the female's acceptance behavior. Pairs often remained *in copula* for 1–4 hours, with the abdomen of the female sometimes elevated. Males usually remained atop the female after copulation. She was observed to dislodge the male by a side-to-side wriggling, a behavior displayed by locust leafminer females. In *S. rosea*, multiple matings were frequent, with one pair mating seven times in nine days. Mating in *O. dorsalis* also is characterized by an absence of prolonged courtship. This species exhibits rapid pair formation with the male often inserting his aedeagus within 30 seconds, long copulations followed by postcopulatory "escort" behavior, and multiple matings (Fritz, 1983; Kirkendall, 1984).

The preoviposition period was not determined. Oviposition began in nature during late May or early June, and eggs were present until early July. Eggs were laid singly on the adaxial surface, almost always near the leaflet edge and camouflaged by prior or subsequent adult feeding damage (Fig. 2). In preparing an oviposition site, the female apparently gnaws the upper surface, then deposits an egg in the slight wound thus made. In the laboratory nearly all eggs were laid at night. The brownish egg, 0.74–0.96 mm long ($\bar{x} = 0.87 \pm 0.02$) and 0.46–0.60 mm wide ($\bar{x} = 0.53 \pm 0.01$) ($n = 10$), is not covered with excrement as in *O. dorsalis* (Chittenden, 1902; Dominick, 1938) and *Baliosus nervosus* (cited as *B. ruber*) (Hodson, 1942), but partially coated with a thin cementlike material so that chorionic sculpturing is visible. In withdrawing her ovipositor from this protective substance, the female leaves a distinct spine on the egg surface (Fig. 3). From the lower surface of a leaflet, the oviposition site is marked by a tiny spot of necrotic tissue. The statement that eggs of *Sumitrosis* "are laid in clusters of 3–7 on a leaf or leaflet" (Ford and Cavey, 1985) is inaccurate for *S. rosea* and may not hold for any member of the genus.

In contrast, eggs of the locust leafminer usually are deposited in masses of 3–5 (rarely 1–6) on abaxial surfaces of black locust leaflets, with clutch size averaging



Figs. 2, 3. *Sumitrosis rosea*. 2, Egg on upper surface of black locust leaflet near adult feeding injury. 3, Scanning electron micrograph of egg showing spine (black arrow denotes tip of spine).

4.10 in nature and 3.70 under laboratory conditions (Fritz, 1983). An egg mass is visible on the adaxial surface as a brown spot that superficially resembles an egg of *S. rosea*.

In the field, mating pairs of *S. rosea* were observed until mid-June. The fecundity of 11 field-collected females averaged 72.8 ± 22.44 (range = 16–224). Fritz (1983) reported a mean fecundity of 110.6 for *O. dorsalis*. The mean incubation period was $8.3 \text{ days} \pm 0.57$ ($n = 200$), which compares with an average of 10 days for locust leafminer ($n = 110$ egg masses) (Dominick, 1938). Newly hatched larvae initiated mines on the upper leaflet surface rather than lower surface as in *O. dorsalis*. Mines containing first instars were observed in the field by 12 June 1985 when some second instars of *O. dorsalis* were found; one week later first instars still were the only larval stages of *S. rosea* present. First-instar larvae were found until early to mid-July. In the laboratory the first stadium averaged $5.3 \text{ days} \pm 0.45$ (range = 5–7, $n = 14$). Mines of *S. rosea*, which closely resemble those of *O. dorsalis*, are roughened, blisterlike or parched, and visible from both surfaces. They usually were restricted to one longitudinal half of a leaflet, with both halves sometimes mined toward the apex. Because eggs are laid singly (occasionally there was more than one under laboratory conditions), larval migration was not observed as frequently as in *O. dorsalis* in which 3–5 larvae occupy an initial mine. Larvae of all stages, however, may vacate a mine, especially on a tiny leaflet. Migrant larvae of both species began mining new leaflets on the adaxial surface.

Second instars were present from about late June to mid-July 1985. Based on the rearing of 3 individuals, the second stadium averaged 6.0 days (range 5–7). A few third instars were observed by early July when summer (current) generation adults of locust leafminer were numerous. By mid-July the *S. rosea* population consisted mainly of third instars and pupae, overwintering adults having died between 8 and 18 July; in the laboratory, mean longevity of 9 overwintered adults was $23.4 \text{ days} \pm 5.29$ (range = 1–42). As in *O. dorsalis*, pupation occurred in the larval mine, and pupae, when disturbed, are capable of wriggling. In the laboratory the third stadium and pupal period were each estimated at 5–7 days. Teneral adults remained in mines for 1–2 days before chewing through the brittle epidermis covering the mine and, in the laboratory, fed on unmined areas of the leaflet from which they emerged. Based on averages for the incubation period and first and second stadia, and on approximations for the third stadium and pupal period, the life cycle of *S. rosea* required about 32 days under laboratory conditions, which was slightly less than for *O. dorsalis*. It appeared that 2–3 leaflets were used during larval development compared to 3 or 4 for locust leafminer.

Summer generation adults were observed by 24 July; they were more numerous on 29 July, with emergence continuing into mid-August. A few adults were present on host trees as late as mid-September.

In 1984 and 1985 we did not observe mating or oviposition in the current generation. Under laboratory conditions in 1984, there also was no evidence of a second generation. In 1985 when development of laboratory populations was 3–4 weeks ahead of that in the field, females deposited viable eggs during late July. Although *S. rosea* appears to have a univoltine life cycle, the possibility of a second generation being produced in certain years cannot be discounted.

Our field observations indicated that locust leafminer populations were univoltine in both years, and this species produced a single generation in the laboratory in 1984. Several authors have reported a second brood for *O. dorsalis*, but

Table 1. Comparative life history data for two hispine leafminers of black locust.

Character	<i>Sumitrosis rosea</i>	<i>Odontota dorsalis</i>
Overwintering stage	Adult	Adult
Appearance on host	Late Apr. to mid-May	Late Apr. to early May
Adult feeding	Few plant species	Many spp., including oak, fruit trees
Larval hosts	Leguminosae, mainly black locust, also soybean; Urticaceae	Leguminosae, mainly black locust, also soybean
Oviposition habits	Eggs laid singly on adaxial surface	Eggs in clusters of 3–5 on abaxial surface
Fecundity	$\bar{x}$ = 72.8	$\bar{x}$ = 110.6 (Fritz, 1983)
Incubation period	$\bar{x}$ = 8.3 days	$\bar{x}$ = 10 days (Dominick, 1938)
Larval period	ca. 17 days	$\bar{x}$ = 17.6 days (Dominick, 1938)
Pupal period	ca. 6 days	$\bar{x}$ = 9.6 days (Dominick, 1938)
Generations/year	1	Probably 1

we agree with Ford and Cavey (1985) that the locust leafminer (as well as other eastern hispines) probably is univoltine throughout its range. The delayed emergence of some adults from overwintering sites, with oviposition spread over several weeks, leads to varying rates of development among individuals in a population. In Rhode Island, for example, *O. dorsalis* deposited eggs from early June to early July (Kerr, 1951). An observation of emergence occurring a month after the first appearance of summer adults would suggest a bivoltine life cycle.

The only natural enemies we observed of either hispine species were the mirid *Lopidea robiniae* Knight and a chrysopid, *Chrysopa* sp. On four or five occasions nymphs of *L. robiniae* pierced the epidermis of a mine and appeared to attack larvae of *O. dorsalis* or *S. rosea*; once we observed a nymph with its stylets inserted in an egg mass of *O. dorsalis*. Twice we observed chrysopid larvae preying on *S. rosea* pupae. Weaver and Dorsey (1965) listed predators and parasites of *O. dorsalis* in West Virginia; in Illinois, McPherson (1985) reared three parasitic species (Hymenoptera: Chalcididae and Eulophidae) from *S. rosea* larvae or pupae.

DISCUSSION

Odontota dorsalis and *Sumitrosis rosea* produce similar, blisterlike mines on leaflets of their preferred host, black locust. These chrysomelids of the tribe Chalepini also share a similar, univoltine life cycle, though overwintered adults of the former emerge slightly earlier; thus throughout the season locust leafminer development is advanced 1–2 weeks compared to that in *S. rosea*. The species differ notably in their oviposition habits and egg structure; Table 1 compares and contrasts selected biological traits.

These species commonly co-occur on small black locust trees, with numbers of the locust leafminer usually outnumbering those of *S. rosea*. Their mines are indistinguishable in the field, and the second, less abundant hispine on black locust is often undetected. On most severely mined trees, the scorched appearance of foliage and premature leaflet drop can be attributed to attack by *O. dorsalis*. Because on some trees adults of *S. rosea* are nearly as abundant as those of the locust leafminer, this species also may cause significant injury. Typically, however,

its colonization of black locust only intensifies damage inflicted by this tree's primary pest, *O. dorsalis*.

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SEXUAL BEHAVIOR OF EUMENID WASPS (HYMENOPTERA: EUMENIDAE)

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Abstract. — The sexual behavior of five eumenid wasp species is described. This behavior differs sharply between species, and there is considerable within-species variation. Pairs of *Ancistrocerus antilope* remained together for 0.5–4 h and copulated one to four times. Pairs of *A. adiabatus*, *A. catskill*, and *Euodynerus foraminatus* came together, copulated once, and separated within 1–2 min. Pairs of *Parancistrocerus pensylvanicus* joined, and copulated once within about one min; but remained together for about 12 min and engaged in an elaborate postcopulatory behavior before separating.

The purpose of this article is to describe the sexual behavior of five eumenid wasp species and begin understanding these behaviors in an evolutionary context. It is now apparent that sexual behavior is best understood in terms of the two major aspects of sexual selection: 1) competition between males and its continuation as competition between their ejaculates (sperm competition) within a female's reproductive tract, and 2) female choice of males (Thornhill and Alcock, 1983). Among the eumenids, sexual selection has resulted in diversity with regard to behavior and structures used by males during courtship, the duration of single copulations, repeated copulations by a single pair of wasps, and post-insemination displays.

Newly emerged males of *Paraleptomenes miniatus* (Saussure) remain on their natal nest and mate with a sister (Jayakar, 1966; Jayakar and Spurway, 1966). In this species the sexes remain paired for nearly 2 h, and copulations which last only a few seconds are repeated every 15 to 20 min. Some other eumenids also have siblings mating at their natal nests: *Euodynerus foraminatus* (Saussure) (Cowan, 1979), *Ancistrocerus adiabatus* (Saussure) (Cowan, 1981) and probably *Epsilon* sp. (Smith and Alcock, 1980). In these species, a pair copulates only once for no more than a few minutes.

Species of *Paralastor* and *Abispa* have males that search for mates at wet areas where the females obtain building materials for nests (Smith and Alcock, 1980). Pairs of *Abispa ephippium* (Fabricius) fly together up into vegetation where they usually copulate twice, and following the last copulation the male performs agitated biting and pulling movements on top of the female before they separate. Mated pairs of *Paralastor* sp. copulate once for periods of 2–12 min, and the female may resist the male throughout or accept him quietly.

Some eumenids copulate for extended periods. Rau (1935) observed *Monobia*

quadridens (Linnaeus) mating for periods up to 30 min, and Cooper (1955) reports *Ancistrocerus antilope* (Panzer) copulating for periods of 12 to 28 min. In the course of various studies, I have had opportunity to make notes on the mating behavior of five eumenid wasps: *Ancistrocerus antilope*, *A. catskill* (Saussure), *A. adiabatus*, *Parancistrocerus pensylvanicus* (Saussure), and *Euodynerus foraminatus*. My observations not only reveal additional interspecific variation in mating behavior among the Eumenidae but also indicate significant intraspecific variation.

METHODS

Wasps were obtained using trap-nests (Krombein, 1967) placed in rural areas of Kalamazoo, Emmet, and Cheboygan Counties, Michigan. The nests were open and the wasps were reared to adulthood in individual chambers. After eclosing as adults, they were segregated by sex and kept for several days in holding cages until used for mating experiments. While in the holding cages the wasps fed on sugar water.

I observed mating by placing one male and one female into cages approximately $30 \times 30 \times 30$ cm. The cages had the top and one side made of glass and three sides of netting. Notes were recorded with a tape recorder. Pairs were left together in the cage until it was apparent that a male would no longer approach a female, a female successfully rejected a male, or they copulated and separated. These are behaviors that would have resulted in freely flying wasps becoming widely separated. Some *A. adiabatus* and *E. foraminatus* were not removed from their natal nests for rearing. Instead, they were reared and marked within their nests (Cowan, 1979, 1981). The nests were then placed outdoors, and the activity of freely flying wasps was observed. I use "courtship" to refer to the activities between a male's mounting and intromitting a female. "Active courtship" refers to periods during courtship when males were engaged in active behaviors that seemed to function in stimulating females. "Inactive courtship" refers to periods during courtship when males simply rode quietly on females. "Copulation" refers to the period of intromission when the genitalia were linked.

RESULTS

Typically, when a male and female were placed together into a cage, the flying male oriented toward the resting or flying female and pounced on her dorsum. When mounted, the male was dorsal on the female facing the same direction. Unreceptive females of *A. catskill*, *A. adiabatus*, and *E. foraminatus* exhibited a distinct rejection behavior consisting of vigorous side-to-side rotation of her thorax around her longitudinal axis while curling her abdomen forward ventrally. This caused courting males to depart quickly. Receptive females tended to extend and lift the tips of their abdomens prior to linking genitalia. For most other aspects of mating, the species showed differences.

Ancistrocerus antilope (Panzer)

From a total of 75 pairings of *A. antilope*, 15 produced no mating behavior because the male did not approach the female. In 29 trials, the male oriented toward a female, mounted her, and either broke off contact immediately ($n = 11$) or courted and attempted copulation but eventually dismounted without mating

Table 1. Number of copulations per pair and mating duration (min) in *Ancistrocerus antilope*. n = sample size; $\bar{x}$ = mean; s = standard deviation.

Number of Copulations per Pair	n	Mean Duration of Pairing	Duration of Individual Copulations							
			First		Second		Third		Fourth	
			$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s	$\bar{x}$	s
1	7	29	23	13	—	—	—	—	—	—
2	20	88	30	6	30	9	—	—	—	—
3	2	145	27	15	28	6	26	6	—	—
4	1	245	27	—	40	—	44	—	34	—

(n = 18). In the 18 cases when males attempted but failed to copulate, 13 pairs were together for less than 5 min (mean, 1.3 ± 1.2 min), but on five occasions, the wasps remained together for 17, 20, 375, 240, and 237 min before separating. Females of *A. antilope* did not exhibit the vigorous rejection behavior observed with some other species. Sometimes they did shake from side to side during courtship, but this did not generally cause males to leave, and often the pair went on to copulate.

Thirty-one pairings resulted in copulations. Table 1 shows the number of copulations per pair, the total time wasps were paired, and the length of individual copulations for 30 matings. A mounted male maintained his hold on a female with his forelegs around the sides of her pronotum, his middle legs held out to the side, and his hind legs encircling her petiole. Using his antennae, he rapidly tapped and/or stroked the female's antennae (so rapidly that I could not determine the rate), but unlike some other species the antennal play did not seem to have any regular motion or periodicity. Sometimes, as a male fluttered his antennae, they appeared not to touch the female. In response, females held their antennae straight up.

While antennating a female, a male drew his abdomen forward so that its tip touched the side of her basal abdominal segments, he extruded his genitalia, and then stroked them down the side and underneath the female's abdomen. When his genitalia reached the tip of her abdomen, he tried to insert them into her genital chamber. The aedeagus and brushlike digitus (Snodgrass, 1941) of his genitalia were the structures that touched the females. The parameral spines were extended and kept clear of the female. Males repeated this probing behavior every few seconds, first from one side of the female's abdomen and then from the other, until achieving intromission. Males that did not successfully initiate copulation within 30–60 s broke off active courtship and simply rode on the female while she crawled or flew about. The males then resumed courtship after a varying period. If a male successfully linked genitalia, he remained dorsally on his mate but his abdomen's tip twisted about 90 degrees to the side to join with the female which also twisted her abdomen laterally about 90 degrees, thus bringing their abdomens venter to venter. During copulation, males embraced females with their middle legs in addition to the other pairs. This may have prevented females from flying. I never saw copulating pairs fly.

Some copulations proceeded with both male and female practically motionless. At these times, females stood with their antennae down, somewhat out to the

side, and males held their antennae in front of the female's face and waved or twitched them slightly. Quiet copulations contrasted with times when the wasps, particularly females, seemed agitated. Females kicked with their hindlegs at the tips of males' abdomens; and with their forelegs at the anterior ends of the males, particularly where they grasped females' prothoraces with their front legs. The females often walked about and wriggled their abdomens from side to side. These actions by females seemed to be attempts to dislodge males, and sometimes they seemed to cause the males to buzz their wings—perhaps in order to retain their hold on the females. Wasps exhibited all states between calm and agitated copulation.

The struggling during copulation did not follow a discernible pattern, but 15 pairs performed a stereotyped periodically repeated set of behaviors that lasted for 1–3 min midway through their last copulation. I saw it performed by three pairs that copulated once, 11 pairs that copulated twice, and by one pair that copulated three times. At these times, females appeared agitated as described above. Males started to tap at the females' raised antennae, and females gradually lowered their antennae. Then, simultaneously, the female wriggled her abdomen, both wasps raised their antennae straight up, and the male buzzed his wings momentarily. As a female wriggled, she rotated her abdomen so that the tip was no longer turned to the side, but was curled ventrally and drawn directly underneath the rest of the abdomen. Thus, her abdomen was not turned to the side and the male twisted his body even further around underneath his mate. As the wasps assumed this posture, their bodies seemed to stiffen and they remained motionless for a few seconds. The males lowered their antennae, waved them in front of the females, the females lowered their antennae, started to move about a little, relaxed their abdomens allowing them to rotate to the side, and the sequence was repeated at about 10 s intervals.

Copulation ended without an apparent struggle, and the unlinking of genitalia was not accompanied by separation of the pair. Once unlinked, several things might happen. Some males rode for a few seconds or minutes before flying away. Other times, after a period of inactivity, males initiated courtship behaviors identical to those before the first copulation and they either recopulated or the males flew away. The interval between successive copulations was 24 ± 25 min.

In the field, I have not seen *A. antilope* males frequenting nest sites where they might mate with emerging virgin females or with nesting females. Males were, however, common around flowers, and their behavior indicated they were searching for mates rather than feeding (Cowan and Waldbauer, 1984). They flew from flower to flower where they hovered or circled without landing. I once observed on a goldenrod inflorescence a female that was mounted by one male when a second male landed on top of them. The trio tumbled to the ground, the second male was displaced, and the female with the first male still mounted flew about 10 m up out of sight into nearby trees. It seems likely that males locate females at flowers, but once pairs have formed, they fly to less conspicuous sites for their extended copulations.

Ancistrocerus catskill (Saussure)

I observed 12 matings by *A. catskill* and timed the events in 11 of the copulations. Courtship was brief (9.5 ± 8.6 s) in 10 of the matings, but in one instance the male rode the female for 9.5 min before they linked genitalia. In eight pairings,

both sexes held their antennae erect and motionless, but in the other three the males tapped or stroked the female's antennae irregularly. Males simply probed with their genitalia at the tips of the females' abdomens; there was no repeated periodic abdominal stroking as seen in *A. antilope* or periodic probing as seen in *P. pensylvanicus* (see below).

As soon as a pair linked, a male released his leghold on a female's thorax and fell back behind her, attached only by his genitalia. A calm period followed (8 ± 6.5 s) while the female stood quietly and the male was immobile. This ended when females started wriggling and kicking at the tips of their abdomen, sometimes resulting in males being flailed about and banged against the substrate. Throughout this struggling by females, which lasted 72 ± 38 s, males remained impassive. In three copulations, the females brought their abdomens forward under their bodies and bit at the tips of the males' abdomens. Apart from the exceptional pairing with the long courtship, males and females of *A. catskill* were together for only 91 ± 33 s ($n = 10$) and their genitalia were linked for only 80 ± 38 s ($n = 11$). On four occasions, males remounted, but the females rejected them as described above.

Ancistrocerus adiabatus (Saussure)

I observed 12 matings by this small eumenid. Half the matings involved caged pairs, and the other half involved freely flying wasps near trap-nests where young adults were emerging. The events in all matings were similar, and I timed the events in six pairings. Mating by *A. adiabatus* is much like that of *A. catskill*, the primary difference being that *A. adiabatus* copulates more quickly.

As soon as a male mounted, he probed from the side at the tip of a female's abdomen with his genitalia and tapped or waved his antennae irregularly in her face. They quickly linked genitalia (within 12.4 ± 8.2 s); males immediately released their leg-hold, and fell back behind their mates. In two matings, the males waited 8 and 10 seconds after linking before falling back, and during this period both wasps were quiet with their antennae held erect. As with *A. catskill*, males dangling by their genitalia were motionless. Within 15 s after a male dropped back, females started kicking at the tips of their genitalia and wriggling their abdomens so that males were thrashed about. All the copulations ended when the females drew their abdomens forward and bit at the males. The wasps were paired for 41 ± 8.5 s, and they copulated for 31 ± 12 s. Once inseminated, females always rejected males that attempted mating.

Males of *A. adiabatus* return to the area of their natal nest as do males of *E. foraminatus* (Cowan, 1981), but *A. adiabatus* males did not regularly visit or defend nest entrances where virgin females were emerging. However, I did observe copulations by freely ranging wasps near nests that involved known siblings.

Unlike some other species of hole nesting eumenid wasps, males of *A. adiabatus* do not always develop more rapidly and emerge from the nest before their sisters. Occasionally, both sexes reached adulthood at the same time, the partitions between cells were broken down, and the adults had contact some time before exiting the nest. I suspect that sometimes siblings mate inside their nests before emerging.

Parancistrocerus pensylvanicus (Saussure)

My observations of mating by *P. pensylvanicus* are based on six females and one male from a single nest. The male courted all of the females but copulated

with only two. After the male mounted, pairs sometimes ($n = 2$) flew together, or the male immediately began courtship involving antennal play and a swiping probing motion at the tip of her abdomen with his partially extruded genitalia. The female stood with her antennae raised, and the male stroked them very rapidly two or three times (so rapidly that I was unable to be sure how many strokes were involved) and then paused momentarily with his antennae held erect before another series of rapid strokes. The bursts of antennal stroking came at about 1.5 s intervals. The abdominal probing differed from that of *A. antilope*. Rather than stroking the side of the female's abdomen, the male *P. pensylvanicus* only tapped or probed at the tip of a female's abdomen alternately from one side and then the other at 1.6 s intervals.

One pair did not copulate but remained together for 21 min. During this period, the male courted actively several times for about 1 min each. The remainder of the time, he simply rode on the female or the pair flew about the cage. When the male did court actively, he probed with his genitalia, and the female moved the tip of her abdomen to the side—away from the tip of his abdomen. In another trial, the male courted for about 1 min with similar results before dismounting. In the other two unsuccessful pairings, the male pounced on a female but quickly disengaged—once after the female wriggled her body, and the other time for no apparent reason.

In the two pairings that involved copulations, the male rode the female for about 10 s before starting antennal stroking and abdominal probing, and after about 35 s of active courtship they linked genitalia. After coupling, the male remained dorsal on the female with his abdomen positioned directly over the female's abdomen and curled ventrally to meet her genital chamber from the posterior ventral aspect. The male also continued to stroke the female's antennae in the same fashion used during courtship. He continued this behavior for 22 s in one case and 18 s in the other and then released his leg hold on the female so that he fell back attached only by the genitalia. The female immediately drew her abdomen forward ventrally and started biting and kicking at the tips of their abdomens. The struggling lasted for 15 and 8 s in the two copulations, and then their genitalia separated. As they unlinked, the male obtained a purchase on the female's abdomen with his legs and crawled back to the dorsal position.

After remounting, the male rode quietly on the females for 27 and 32 s before starting postcopulatory behavior. This behavior was very different from precopulatory courtship and did not seem to be an attempt by the male to remate. He raised his antennae, head, and abdomen and then brought them down seemingly forcefully on the female. The male repeated this behavior about five or six times a second for 2–3 s, paused for 5 to 20 s, and then performed another series. As the male bounced on the female, his mouth parts were between her head and thorax, his antennae tapped at about the middle of her flagellum, and his abdomen came down directly or slightly to the side of hers. Occasionally, the wasps flew together during postcopulatory activity. The male behaved this way for 12 and 13 min after the two copulations before dismounting.

Euodynerus foraminatus (Saussure)

I watched over 60 copulations by *E. foraminatus* and I timed the events in 26. Most of these observations involved freely flying wasps but seven pairs were

confined in cages. When mounted, a male grasped a female just under her tegulae with his forelegs; his middle legs were usually held out to the side but sometimes grasped the sides of a female's propodeum. His hind legs passed between her wings and clasped her basal abdominal segment.

Using the hooked apical segments of his antennae, a male simultaneously drew both of a female's antennae upward and stroked the length of her flagellum. This was repeated about once per second. At the same time, he probed with his abdominal tip around her abdominal venter and attempted to link genitalia. After mounting by a male, linkage occurred in 17 ± 38 s, and copulation proceeded quietly for 19 ± 10 s. During this quiet period, a male remained mounted, continued antennal stroking, and occasionally buzzed his wings. Females remained calm with their antennae held erect, or took a few steps. This quiet stage ended, and a struggle stage began, by movements of a female that started as side to side wriggling of the abdomen. These movements gradually became more vigorous, and a female used her hind legs to kick the male and to pry between their abdomens. Meanwhile, the male continued antennal stroking and flipped his wings occasionally, apparently to maintain balance. Struggling lasted 61 ± 31 s. When copulation terminated, males flew up from their mates.

The period between mounting and intromission is generally very short (about 5 s); however, for three copulations, all involving the same male, this period was 61, 97, and 170 s. I observed no other matings by this male. These copulations were the only three of the 60 I watched in which the male did not immediately begin antennal stroking and probing with his abdomen. This male simply mounted and rode passively on the females before starting active courtship, and then the copulations proceeded normally. The three females involved groomed or walked about during this precopulatory period, and one flew to a leaf about 50 cm away with the mounted male.

The struggle phase of one copulation did not end with the male flying up, but with the male releasing his hold with his legs and falling back suspended only by the genitalia. The female turned and bit the male on the tip of his abdomen, and the pair separated immediately. Falling back and hanging by the genitalia is typical when a copulating pair is disturbed by an intruding male (Fig. 1). The intruder lands on the copulating male which releases his grip and falls back. The intruder may then fly up, mount the female, stroke her antennae, and probe with his genitalia, while the original male remains firmly coupled to the female. If an intruder arrives before a male and female are securely linked, he may prevent copulation and cause the female to fly away unmated. Mated females always rejected males that attempted courtship.

DISCUSSION

Mating behavior can be divided into three stages: 1) courtship; 2) copulatory behavior, including duration of copulation, number of copulations per pairing, position assumed by the sexes, and which sex is most active in terminating copulation; and 3) postcopulatory behavior. All stages of mating have probably been influenced by sexual selection acting thru male-male competition and female choice of males (Thornhill and Alcock, 1983). Once a male and female have come together, male-male competition may occur as males attempt to displace each other on the female, and it may continue as sperm competition, within a female's

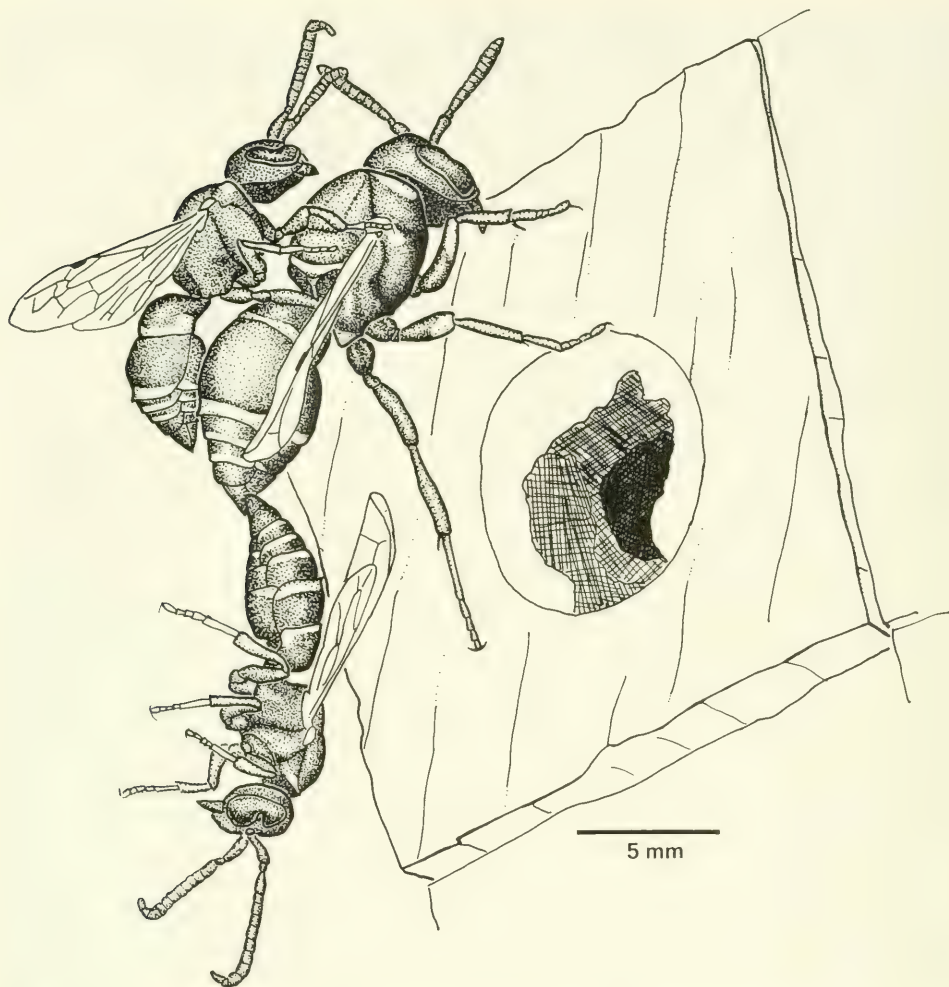


Fig. 1. A disturbed copulation of *Euodynerus foraminatus*. The wasp standing on the front of the trap-nest is a female. The two smaller individuals are males. The male hanging by his genitalia mounted the female and initiated copulation as she emerged from the nest. The male grasping the female is an intruder.

reproductive tract, between the ejaculates from different males. Females may exercise choice by simply making themselves available to favored males, by actively rejecting some males that court, or by remaining sexually receptive until having mated with a "choice" male. In the latter case, females may effectively "choose" the last male by allowing his sperm to fertilize her eggs.

Courtship.—Courtship communicates a variety of information, including species and sexual identity and information about the "quality" of potential mates. Consequently, some features of courtship may have evolved in the context of runaway sexual selection (Fisher, 1958). Eberhard (1985) argues that structures used by males to stimulate females during mating behavior will be most subject to runaway sexual selection, will evolve rapidly, and will thus be useful taxonomic characters. This seems to be the case for eumenid wasps. Antennal play by the male during

courtship is common, and the shape of the apical antennal segments on male eumenids is frequently used by taxonomists as a diagnostic character (Bohart, 1939a, b, 1940, 1948; MacLachlan, 1980). Males of *A. antilope* stroke females with their genitalia but males of *A. catskill* and *A. adiabatus* do not. Within the genus *Ancistrocerus*, male genitalia are rather uniform with the exception of *A. antilope* which has distinctive male genitalia (Bequaert, 1944). Males of *P. pennsylvanicus* tap females with their genitalia during courtship, and for species in this genus male genitalia are distinctive (Bohart, 1952).

Duration of pairing.—Because pairs of some species of Eumenidae mate and separate within a minute, it seems unlikely that the longer matings exhibited by other species are necessary simply for sperm transfer. Thornhill and Alcock (1983) discuss several factors that could prolong copulating in insects. In addition to sperm, males may transfer nutrients to the female. If females mate with more than one male, then male-male competition may extend to competition between the ejaculates of the different males (sperm competition) within females' reproductive tracts. If males remove stored sperm from a female's reproductive tract or displace it with their own, extra time would be required. Or, a male might maintain contact with a female beyond the period needed for insemination to prevent other males from mating with her and displacing his sperm. Prolonged mating may induce non-receptivity of females.

The data needed to test these hypotheses for the wasps I watched are lacking. However, the species that mate quickly (*E. foraminatus*, *A. adiabatus*, and *A. catskill*) have monogamous females, and the species with the longest copulations (*A. antilope*) has females that do mate repeatedly with different males (Cowan and Waldbauer, 1984). This supports the hypothesis that extended copulation in these wasps has resulted from competition between males, sperm competition, or both.

Post-insemination displays and repeated copulations.—That males of *P. pennsylvanicus* remain mounted on the female and engage in complex behaviors after completing insemination is surprising. Having transferred sperm, such activities would seem to be a waste of time, and one might expect the male to depart directly and resume other vital activities. Similar behaviors are known for a variety of Hymenoptera: *Abispa ephippium*, also in the Eumenidae (Smith and Alcock, 1980), a number of Chalcidoidea (Assem and Visser, 1976; Gordh and DeBach, 1978), and in the anthophorid bee *Centris pallida* (Alcock and Buchmann, 1985). Experiments with the pteromalid *Nasonia vitripennis* (Assem and Visser, 1976) and *C. pallida* (Alcock and Buchmann, 1985) show that post-insemination displays in these insects are important for inducing unreceptivity in the females. Normally, following a complete mating with post-insemination display, females of these two species reject the advances of additional males. However, when a male is prevented from performing his post-insemination display, females will mate again even though they had acquired sperm from the first male. Alcock and Buchmann (1985) speculate that the first male to mate with a female is sometimes genetically inferior. Should such a male be prevented from the post-insemination display and supplanted by a stronger male, then the female would obtain sperm from the genetically superior male. Thus, requiring post-insemination displays from males is viewed as an adaptation by females that increases their chances of obtaining a mate with "good genes."

Three species of eumenid are known to have multiple copulations for each pairing; *A. ephippium* (Smith and Alcock, 1980), *P. miniatus* (Jayakar, 1966), and *A. antilope*. Because the lifetime fecundity of females is low (probably not more than 25 eggs require fertilization (Cowan, 1981)), and because other closely related species mate only once, it seems unlikely that repeated copulations are needed to supply a female with adequate sperm. In fact, the stereotyped antennal movements and tensing of bodies observed during the last copulations by pairs of *A. antilope* suggest that physiological activities during the separate copulations may be different. Possibly, the repeated copulations are a means for males to access female receptivity: males attempt and engage in repeated matings until the female becomes unreceptive, thus decreasing the likelihood that the female will soon mate with another male. Repeated copulations by *A. antilope* may be comparable to the post-insemination displays of other Hymenoptera. Females may be less likely to remate quickly if a male demonstrates his "staying power" and thus "good genes" by remaining mounted and copulating repeatedly.

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OBSERVATIONS ON THE BIOLOGY OF TWO SPECIES OF
ORASEMA (HYMENOPTERA: EUCHARITIDAE)¹

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Abstract.—Brief descriptions of life history are given for *Orasema coloradensis* and *Orasema viridis* from Idaho and Arizona, respectively. *O. coloradensis* was reared from nests of *Formica subnitens* and both species of *Orasema* were found in association with thrips. Descriptions of the first-instar larvae are made and the larvae compared to other Eucharitidae.

Members of the genus *Orasema* Cameron, like other members of the family Eucharitidae (Hymenoptera: Chalcidoidea), are parasitic upon ant pupae. Adult females lay their eggs into plant tissue, away from the host, and the active first-instar larvae seek adult ant hosts for transport back to the nest (Clausen, 1940). Wheeler (1907) published the first account of the in-nest habits and gave host records for three species of *Orasema*. He provided a sketch of the planidium of *O. viridis* Ashmead, a parasite of *Pheidole kingi instabilis* (Emery), and illustrated the later larval instars in detail. Wheeler and Wheeler (1937) supplied further information on the larval development of two other species, *Orasema sixaolae* Wheeler and Wheeler and *Orasema costaricensis* Wheeler and Wheeler, which parasitize the ants *Solenopsis tenuis* Mayr and *Pheidole flavens* Roger, respectively.

The out-of-nest habits of *Orasema* sp. (near *aenea* Gahan) were first described by Parker (1942) in Argentina. He wrote that adults deposited their eggs in serpentine rows into leaves of a *Muehlenbeckia* (Polygonaceae) and provided descriptions and figures for the planidium and egg (one egg per puncture) as well as details on the oviposition behavior. Das (1963) supplied similar information for *Orasema assectator* Kerrich, which is parasitic on a species of *Pheidole* in India. Again, eggs were deposited in serpentine rows on tea leaves, and although not stated explicitly, Das implies that a single egg is deposited per oviposition puncture. *Orasema costaricensis* was reported to oviposit into young banana fruits (Kerrich, 1963).

Since the host ants of *O. assectator* do not forage on the tea bushes, Das (1963) mentions a possible role for *Empoasca flavescens* (F.) (tea leafhopper) or *Scirtothrips dorsalis* Hood (tea thrips) as intermediate carriers of the planidia. Other

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associations have been suggested between planidia and thrips but no direct evidence of thrips as necessary intermediates has been made (Clausen, 1940; Wilson and Cooley, 1972).

The almost simultaneous discovery and observation of populations of *Orasema coloradensis* Gahan in Idaho (JBJ, TDM, FWM), and *O. viridis* in Arizona (JMH) offered an opportunity to study the biology of this genus.

METHODS

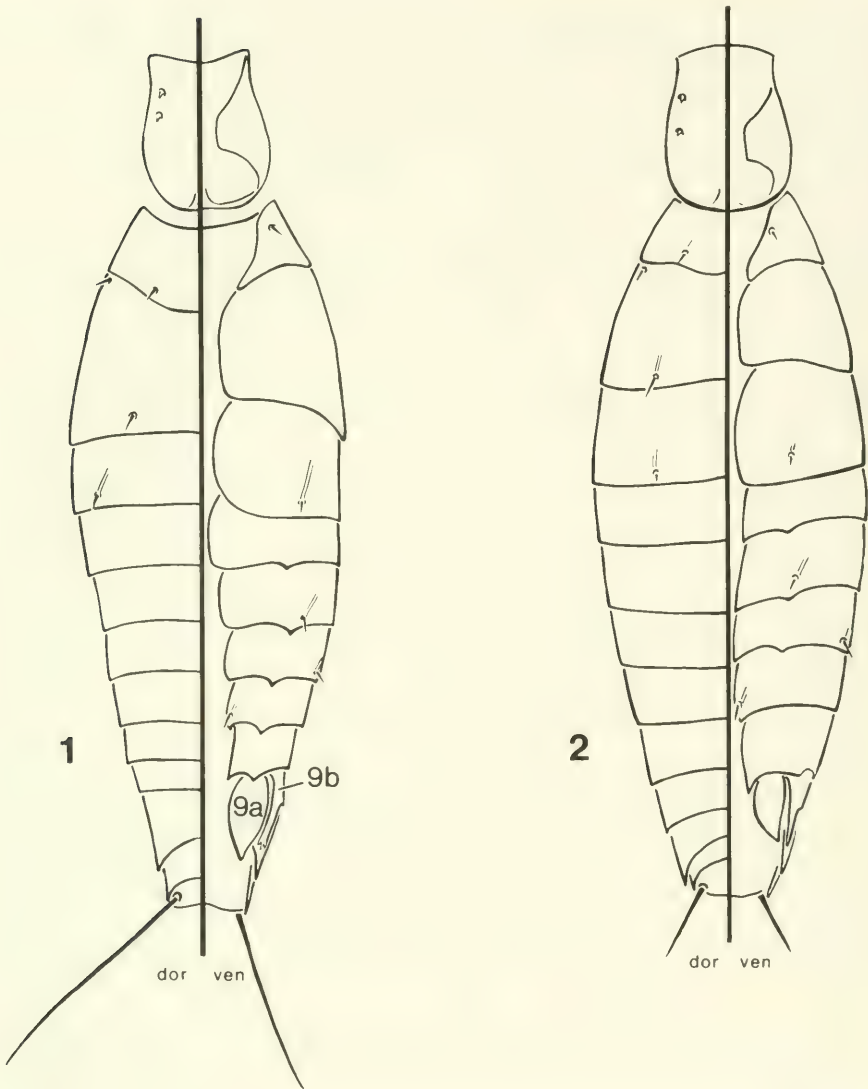
Identification of adults.—The adults were identified through the use of Gahan's (1940) key to the genus *Orasema*. Unfortunately, Gahan's revision may represent only a preliminary treatment of a very diverse and widespread genus. *Orasema coloradensis* is defined as the only *Orasema* with a smooth mesosoma dorsally; however, there are many morphological deviations from the type which could represent distinct species. This makes it difficult to compare the *O. coloradensis* observed by Clausen (1940) in Virginia to those observed in Idaho. Gahan (1940) raised the possibility that *O. viridis*, for which Wheeler (1907) described the life history in the ant nest, may actually be *O. wheeleri* (based on the representative material in the USNM collection), so the two species may be synonymous. To compensate for the taxonomic problems with the genus, representative material from this study have been deposited at the University of Guelph, the University of Idaho and the National Museum of Natural History (Washington, D.C.).

Orasema coloradensis Gahan

Figs. 1, 3, 4

Location and habitat.—Adults were collected from Hells Gate State Park, 5 miles south of Lewiston, Nez Perce Co., Idaho, from 10 June to 7 August, 1983 and 1984. Adult *O. coloradensis* were most commonly swept from gray rabbitbrush, *Chrysothamnus nauseosus* (Pall.) Britt., but they also occurred on green rabbitbrush, *C. vicidiflorus* (Hook.) Nutt. (Asteraceae). Scattered clumps of *C. nauseosus* occur in the relatively undisturbed grasslands of undeveloped portions of the park on the slopes above the Snake River. The vegetation in this area is predominantly grass with the most abundant species being cheat grass, *Bromus tectorum* L., and sand dropseed, *Sporobolus cryptandrus* (Torr.) Gray. The two species of *Chrysothamnus* are the dominant shrubs. Other Astereaceae in the area included: *Erigeron* sp., *Grindelia* sp., *Gutierrezia* sp. and *Haplopappus bloomeri* Gray.

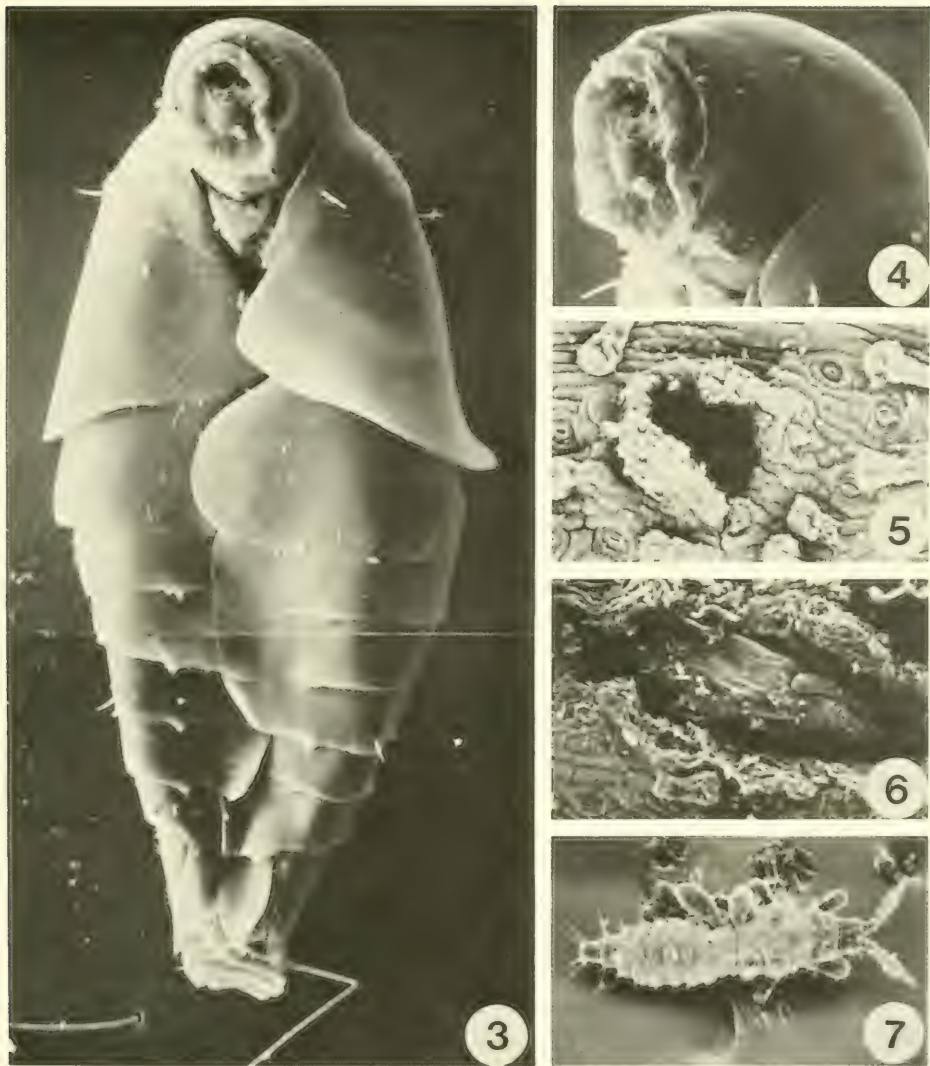
Behavior.—Males and females of *O. coloradensis* were found hovering above rabbitbrush plants, but no mating was observed. Females were often seen flying slowly along suberect branches, apparently searching for oviposition sites. Eggs were usually deposited in leaves, but oviposition into buds and stems also occurred. Oviposition was observed between 9:30 am and 6:10 pm. Ten females were observed for 5 minutes each on 21 July, 1984. A total of 23 ovipositions were observed or about once every 2 minutes per female. An average of 478 [± 18 SD] eggs were found in 10 field collected females that were dissected. Based on field observations and a sample of 100 branches, oviposition occurred more or less sporadically within 19 cm of the branch apices, singly or in a series of 2 or 3 punctures per leaf. One egg was deposited each time the leaf was punctured. Planidia were found on all portions of branch apices, often clinging to a trichome,



Figs. 1, 2. Dorsal and ventral view of the first-instar larvae of *Orasema coloradensis* (1) and *Orasema viridis* (2).

and on nymphs of thrips (*Sericothrips* sp.). As many as 7 planidia were found on a single thrips. Planidia attached to thrips were distinctly larger and more globose than individuals collected from foliage. On two occasions in the laboratory, planidia apparently consumed enough fluid to cause the thrips to shrivel and die. A sample of 100 branches of gray rabbitbrush collected in the field revealed 0–38 planidia/branch (mean of 1.28 ± 4.40 SD). Eggs deposited by adults brought into the laboratory hatched in 4 to 6 days at approximately 22°C, and planidia lived for as long as 18 days [mean of 8.8 ± 3.7 SD, $n = 25$] without access to thrips.

Description of the egg.—The eggs are white with a smooth chorion. The overall length was about 0.12 mm including a 0.05 mm stalk. They are similar to the eggs of other Eucharitidae described by Heraty and Darling (1984).



Figs. 3–7. 3, 4, First-instar larva of *Orasema coloradensis*. 3, Ventral view (1000×). 4, Ventrolateral view of head (200×). 5–7, *Orasema viridis*. 5, Oviposition puncture in involucral bract of *Haplopappus* (300×). 6, Egg in dissected chamber (200×). 7, Two first-instar larvae on immature thrips (65×).

Description of planidium (Figs. 1, 3, 4).—The morphology of the first-instar larva is virtually identical to that described for *Orasema* sp. described in Heraty and Darling (1984) except for the following features: two pairs of dorsal cranial spines (Fig. 4) and four small peg-like sensilla around the anterior margin of the cranium (Figs. 3, 4); presence of a pair of pleurostomal spines fused to the margin of the cranium (Fig. 4); posteroventral margin of tergites IV to VIII are less angulate, and tergites VIII and IX are more modified than was suggested from slide preparations, tergite IXb is finely serrate at apex of ventral extension (Figs. 1, 3). All of the above are variations on the planidium described in Heraty and Darling (1984), and were verified with planidia of *O. viridis* (see below).

Host associations.—The ants known to occur in the area where *O. coloradensis* was collected include: *Formica subnitens* Creighton, *Camponotus vicinus* Mayr, *Pogonomyrmex owyheeii* Cole, *Tapinoma sessile* (Say), *Pheidole californica californica* Mayr, and *Solenopsis (Diplophopterus) molesta validiscula* Emery. Of these species, only *S. molesta validiscula* has been reported as a host for *O. coloradensis* (Wheeler, 1907). *Pheidole bicarinata vinelandica* Forel is the other previously recorded host for *O. coloradensis* (Wheeler, 1907).

The only positive indications of a host-parasite association involved the *Formica*. Excavation of ant colonies of all genera and emergence traps placed over *Formica* colonies revealed adult *O. coloradensis* only from nests of *F. subnitens* (through both methods). In addition, several planidia were washed from *Formica* workers by shaking in alcohol, and a single planidium was found attached to the conjunctiva at the base of the maxilla of a *Formica* worker. This direct evidence is further supported by observations that *F. subnitens* is by far the most abundant large ant on rabbit brush at this site.

The basic outline given here for *O. coloradensis* is supported by limited observations of another population of the same species (or complex) at the Idaho National Engineering Laboratory (INEL) site in southcentral Idaho. Adults of the INEL population were similar, but not identical, to those collected at Hells Gate State Park. They also were observed ovipositing on gray rabbitbrush and rarely on green rabbitbrush. Planidia have been found on foliage and on *Sericothrips* sp. Though many ants occur in this area, *Formica oreas comptula* Wheeler appears likely to be the host on the basis of its size and abundance on rabbitbrush. The only planidium washed from an ant at this site came from a worker of *F. oreas comptula*.

Orasema viridis Ashmead

Figs. 2, 5-7

Location and habitat.—Adults were collected at two locations in the vicinity of the Southwestern Research Station of the American Museum of Natural History (SWRS), 5 mi W Portal, Arizona, August 17, 1984, and almost always in association with a small, yellow-flowered Asteraceae, *Haplopappus* sp. On Herb Martyr Rd. above SWRS, the plants (and adults) were restricted to a narrow band just along the edge of the gravel road. The section of road where adults were collected was open with mixed species of grass on one side and a drywash slope on the other. The second location was on the grounds of SWRS, where *Haplopappus* sp. occurred in patches in well-travelled and mowed areas. *Orasema viridis* was also collected on the SWRS grounds from a dense stand of *Viguiera* (Asteraceae) and also on *Spheralcea* (Malvaceae), but were found in largest numbers on *Haplopappus* sp.

Behavior.—Both males and females of *O. viridis* were collected from *Haplopappus* sp., although no mating was observed. While ovipositing, females were oriented head down on the unopened flower buds of *Haplopappus* sp., with oviposition lasting several seconds. Upon completion, females would either reorient themselves on the same flower bud or fly to another plant. Occasionally females would oviposit on the same involucre bract just below the last puncture. Each female made a single puncture in the upper third of the involucre bract (Fig. 5) on the flower head and laid a single egg in the smooth chamber hollowed out by

the ovipositor (Fig. 6). The egg is oriented with the stalked end upwards. On the SWRS grounds, where *O. viridis* was abundant, all of the flower heads had at least one oviposition puncture and many had punctures in a large proportion of the involucre bracts on a single head. The planidia were found on the opened flower heads either among the involucre bracts or more commonly on the surface of the flower disc. No planidia or empty eggs were found on the unopened flower buds, but this was probably a reflection of the amount of time that the bud had been developed and available for oviposition. Several immature thrips were found in the flower heads, with attached planidia (Fig. 7).

Description of egg (Fig. 6).—The eggs are white with a smooth chorion. The overall length was about 0.13 mm. Caudal stalk less than half length of egg body with a small bulbous apical thickening. Similar to the egg described for *O. coloradensis*.

Description of planidium (Fig. 2).—Identical to the planidium of *O. coloradensis* except for the following features: the two pairs of dorsal cranial spines are smaller; the extended apex of tergite IXb is acute and not serrate; the caudal cerci are rigid and equal to the dorsal length of only 2–3 terminal tergites.

Host associations.—No direct associations were made with any ant hosts. In the area of both locations cited above, colonies belonging to several genera of ants (*Acanthomyops*, *Aphaenogaster*, *Camponotus*, *Odontomachus*, *Solenopsis* and *Trachymyrmex*) were excavated but none contained *Orasema*. However, there was a species of *Formica* (*fusca* group) commonly found walking over the open flower heads on the SWRS grounds which was of a suitable size to act as a host of this species of *Orasema*. There were also some stray *Pheidole* walking on the ground among the plants. No nearby colonies of *Formica* or *Pheidole* could be located for excavation.

DISCUSSION

Ant hosts.—The two species of *Orasema* observed in this study were found to oviposit mostly on restricted species of Asteraceae, and *O. coloradensis* was reared from the nest of *Formica subnitens*. Previously, *Orasema* spp. have been reared from only the ant genera *Pheidole* and *Solenopsis* (Wheeler, 1907; Wheeler and Wheeler, 1937; Clausen, 1940; Gahan, 1940; Das, 1963). The rearing records from *Solenopsis* may be accidental, as members of the subgenus *Diplorhopterum* are small thief ants which live in close proximity to, and steal brood from, colonies of other ants. Wheeler (1907) states that at least one colony of *Solenopsis molesta* was “living in cleptobiosis with a large colony of *Formica ciliata* Mayr,” although he feels that the *Orasema* were probably parasites of the sexuals of *Solenopsis* (the only *Solenopsis* pupae of a proper size).

Plant hosts.—The plant hosts utilized for oviposition have been recorded as *Ilex paraguayensis* Hooker (Aquifoliaceae) for *Orasema aenea* Gahan, *Stylosanthes biflora* (L.) B.S.P. (Fabaceae) and *Ceanothus americanus* L. (Rhamnaceae) for *O. coloradensis* (in Virginia), *Casearia spinescens* Griesbach (Flacourtiaceae) for *Orasema smithii* (Calusen, 1940), and tea leaves (Celastraceae) for *O. assecator* (Das, 1963). Our observations represent the first report of *Orasema* ovipositing into Asteraceae, although, adults of *Orasema cockerelli* Gahan and *Orasema neomexicana* Gahan have been collected from *Bigelovia* and *Gutierrezia*, two genera of Asteraceae closely related to *Chrysothamnus* and *Haploppapus*.

Thrips association.—An association between the planidia of Eucharitidae and thrips (as an intermediate carrier) has been suggested by Das (1963) and Clausen (1940). Observations on the eucharitid *Psilogaster antennatus* Gahan showed that the females will only deposit their eggs in association with the eggs of the thrips, *Selenothrips rubrocinctus* (Giard) (Clausen, 1940). No association could be made between *Psilogaster* and an ant host. In both species of *Oreasema* dealt with here, the planidia were commonly found attached to nymphal thrips and, in one case, the planidia appeared to have fed on the thrips.

Oreasema coloradensis apparently oviposits from mid-June to mid-August. *Formica* colonies often occur at the base of rabbitbrush plants, but the ants spend little time foraging on rabbitbrush, unless aphids or flowers are present. Establishment of aphid colonies is sporadic, thus not a dependable host attractant for *O. coloradensis* planidia. The flowering of rabbitbrush plants at Hells Gate State Park is asynchronous, typically beginning in late July, peaking around 1 September and continuing through early October. This would mean that a planidium could have to wait as long as three months for *Formica* workers to be readily available. Thus, it seems likely that planidia survival would be enhanced by finding an alternate food source, in this case, *Sericothrips* sp., which is common on rabbitbrush.

Morphology.—Discovery of the characters from the planidia discussed above, such as the pleurostomal spines and structure of the terminal tergites, which appear different from the *Oreasema* sp. from Costa Rica (Heraty and Darling, 1984), is the result of finer resolution through SEM techniques. The presence of dorsal cranial spines can be seen on slide-mounted material, and these are definitely not present on the *Oreasema* sp. from Costa Rica. Whether or not these spines can be considered homologous to the enlarged dorsal cranial spines found in *Perilampus* (Heraty and Darling, 1984) can only be left to conjecture. Their use in supporting any relationship between the two groups (Perilampidae and Oraseminae) would require the presence of spines in other Oraseminae, or at least a demonstration that this is the plesiomorphic condition of the subfamily. In general, the larvae support the character states of the Oraseminae, as defined in Heraty and Darling (1984) and also the differences between this subfamily and the Eucharitinae.

The sclerites labelled as tergites IXa and IXb are unique in that they occur side by side. The origin of either tergite underneath tergite VIII could not be resolved. The lack of a dorsal extension of the leaf-like sclerite (IXa) makes it likely that it is not an additional tergite, but is more likely the derivative of another tergite such as IXb. Adults of *O. coloradensis* are distinguished from *O. viridis* largely by the presence of a smooth mesoscutum (dorsally) in contrast to the uniformly alveolate mesoscutum of *O. viridis*. Compared to other nearctic *Oreasema*, the two species are distantly related, yet their larvae are almost identical. Except for the presence of dorsal cranial spines, these larvae are barely distinguishable from the Costa Rican species described by Heraty and Darling (1984). This similarity demonstrates the conservatism of the first-instar morphology, which is similar to that found in other eucharitids.

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NOTES ON THE DISTRIBUTION AND ABUNDANCE OF
GROUND- AND ARBOREAL-NESTING ANTS
(HYMENOPTERA: FORMICIDAE) IN SOME
COSTA RICAN CACAO HABITATS

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Abstract. — The number of species and approximate colony sizes including presence/absence of brood were determined from multiple samples of forty arboreal, rotten cacao pods (*Theobroma cacao* L.) for each of seven widely scattered censuses over a two-year period at one locality (Finca La Tigra) in northeastern Costa Rica. Similar data were obtained for a one-year period (three scattered censuses) for experimental plots of various ground substrates (rotting banana trunk slices, cacao pod husks, leaf litter) in two contrasting cacao habitats (well-maintained cacao "plantation" and "cacao forest") at a different locality (Finca Experimental La Lola) within the same climatic region. Although close to 30,000 ants, representing 10 genera and 16 species, were collected from arboreal pods at La Tigra, there was only 25% faunal overlap with the ground-nesting samples from La Lola. *Crematogaster limata palans* Forel was one of a few "dominant" species in arboreal pods at La Tigra, but was entirely absent in the La Lola ground samples. In each habitat, a few species were dominants, in terms of colony size range and the frequency of occupancy of nesting substrates, and the majority of ant species were "rare." Of about 14,000 ants representing 19 genera and 26 species censused at La Lola about 60% occurred in the cacao forest. The plantation habitat had 12 genera and 16 species. There was overlap in ant genera and species between the two La Lola habitats. The slices of rotting banana trunk supported the greatest number of ant species in both habitats.

Co-occurring ant species within a habitat often exhibit definitive patterns of resource partitioning, within and outside of the tropics (e.g. Brian, 1955; Brieese, 1982; Brieese and Macauley, 1980; Byron et al., 1980; Carroll and Janzen, 1973; Cole, 1983; Jeanne, 1979; Levings, 1983; Levings and Franks, 1982; Melhop and Scott, 1983; Plowman, 1981; Smallwood, 1982; Swain, 1980; Wilson, 1971 and many included references; Young, 1983). Such patterns are known for other insects as well (e.g. Allee et al., 1949; Anderson, 1982; Bahrmann, 1980; Hanski, 1980; Karoji, 1980; Prince and Parsons, 1980; Ranta and Lundberg, 1980; Schmalfuss and Ferrara, 1982). Tropical forests, in particular, are exceedingly rich in ant species (e.g. Ayre, 1977; Evans, 1982; Kempf, 1975; Levings and Franks, 1982; Wilson, 1976a, b). Furthermore, contrasting tropical habitats, such as agricultural plantings and nearby forest, often exhibit pronounced differences in the overall

“species richness” of both ground-nesting and arboreal-nesting ants (e.g. Adams et al., 1981; Banerjee, 1983; Fabres and Brown, 1978; Saks and Carroll, 1980; Samways, 1981, 1983).

The cacao plantation, in particular, both in the New World and Old World tropics, has been contrasted, in terms of its ant fauna, with other habitats (e.g. Evans and Leston, 1971; Jackson, 1984; Leston, 1970, 1973, 1978, 1979; Lieberman and Dock, 1982; Young, 1983). Such studies generally show that tropical forest habitats contain a greater number of ant species than agricultural habitats (e.g. Jeanne, 1979; Leston, 1979; Lieberman and Dock, 1982), although not always (Young, 1983). In this paper I present new data on the distribution and abundance of ant species in contrasting cacao habitats in Costa Rica. Emphasis is placed upon the comparison of ant assemblages associated with a variety of ground substrates as well as that of arboreal, rotten cacao pods within each habitat studied. The data support the contention that abandoned cacao groves, reverting to rain forest, contain a greater species richness of ants than maintained plantations, and that the fauna of arboreal rotten pods is markedly different from that of nearby ground substrates.

MATERIALS AND METHODS

These studies were conducted at two localities, both within the Caribbean watershed zone of Costa Rica: (1) “Finca La Tigra,” near La Virgen (10°23' latitude, 84°07' longitude), Sarapiquí District, Heredia Province (220 m elev.); (2) “Finca Experimental La Lola,” near Siquirres (10°06'N, 83°30'W) (approx. 50 m elev.), Limon Province. Both localities are within the premontane-to-lowland tropical rain forest region of Costa Rica, and experience a short dry season generally in March–April each year (Figs. 1, 2).

Cacao groves at La Tigra are about 35 years old, whereas those of La Lola and adjacent properties date back into the 1920s. The La Tigra site is adjacent to extensive rain forest, including the recently-established Braulio Carillo National Park. In contrast, most of the surrounding area at La Lola is highly disturbed secondary-growth and plantations in varying stages of abandonment.

Between December 1982 and December 1984, I censused ant colonies in samples of exactly forty arboreal, rotten cacao pods from the same approximately 100 × 100-meter area of cacao at La Tigra. Only soft, blackened pods within the size range of a 6 × 2 cm (smallest) to 15 × 7 cm (largest) were collected from trees of mixed varieties, and within a height range of 1.0 to 2.0 m. Pods were placed in large plastic bags and examined at a nearby field station. Each pod was broken apart and its contents examined for ants and associated organisms. For each pod, the presence or absence of adult and brood were recorded. A voucher sample of each ant species was preserved, with a “morphospecies” description. Whenever possible, brood samples were also collected. An attempt was made to estimate the total size of colonies. I used these figures to determine an estimate of ant “biomass,” defined here as the total number of individuals collected at a given census. La Tigra cacao pods were thus examined for ants for a total of seven, widely-scattered census dates, corresponding to “dry” (March), “mid-rainy” (August), and “late rainy” (November) seasons: 1982: 3–4 December; 1983: 2–3 March, 7–8 August, and 10–11 November; 1984: 28–29 February, 3–4 August, and 20 November.

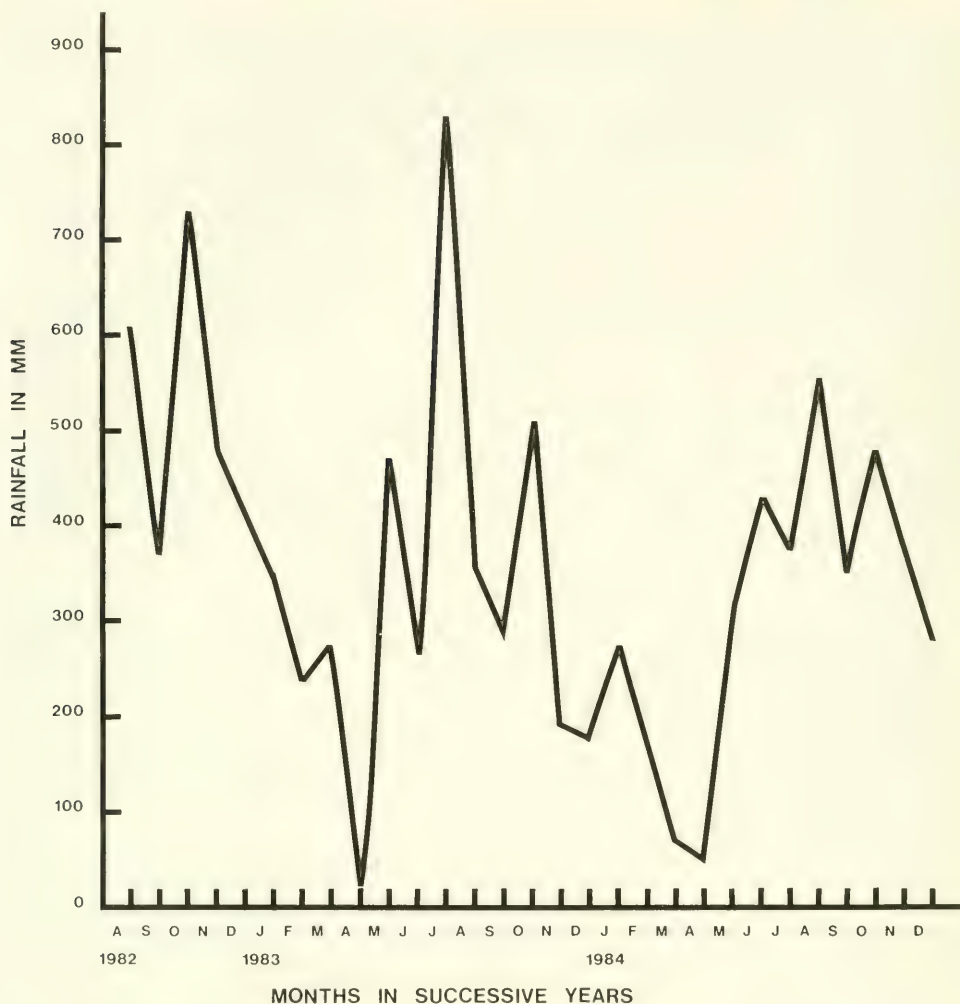


Fig. 1. Monthly rainfall pattern for "Finca La Tigra" in northeastern Costa Rica for the study period (1982–1984). Note dramatic drop in rainfall in March–April each year. The dry season actually begins in mid to late February at this locality. Data courtesy of Dr. J. Robert Hunter, for "Finca La Tirimbina" meteorological station; about 2 km from La Tigra.

At La Lola, I censused ants in ground substrates experimentally distributed in two contrasting cacao ("Matina" variety) habitats: banana trunk slices, cacao pod husks, cacao leaf litter, and for one census (November 1984), arboreal, rotten cacao pods. Ant populations of a well-maintained cacao plantation ("Section 25") of the La Lola farm were contrasted with those of an adjacent, abandoned cacao plantation belonging to Amos Barker. The Barker cacao resembles a forest, and I call it the "cacao forest" habitat, being very distinctive from the well-maintained plantation about 800 m away (Fig. 3). Although the cacao trees in both habitats are about the same age, the "cacao forest" habitat is heavily-shaded due to the presence of a well-developed canopy of forest trees (Fig. 3). The canopy of the "plantation" habitat is broken and uneven (Fig. 3).

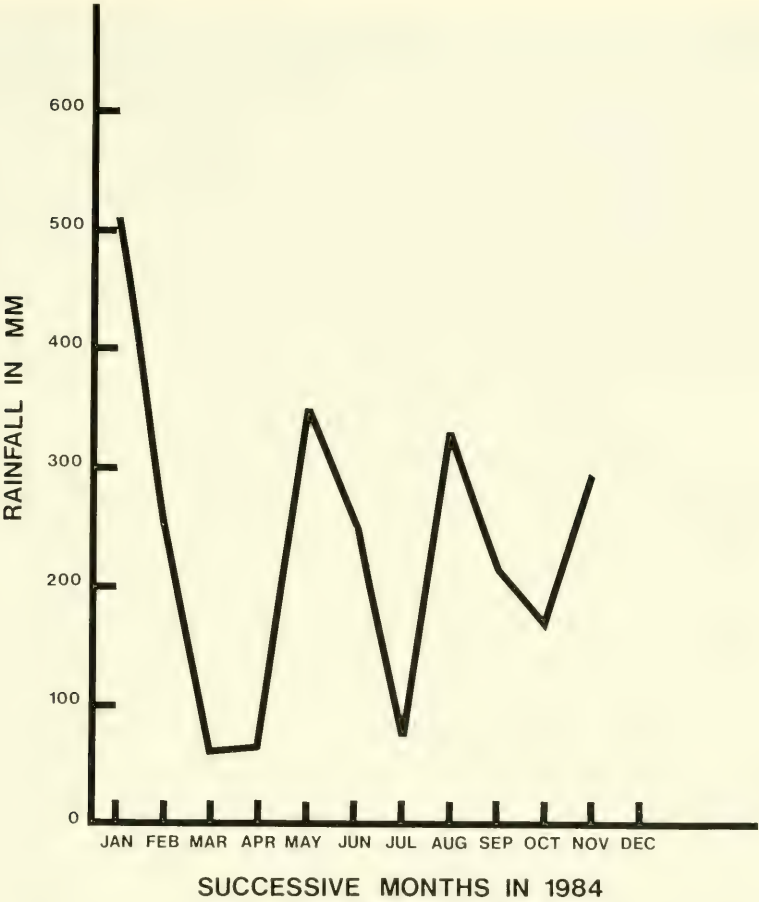


Fig. 2. Monthly rainfall pattern for “Finca Experimental La Lola” near Siquirres, Costa Rica, during the 1984 study period. Data courtesy of C.A.T.I.E. in Turrialba, Costa Rica.

Ground substrates were randomly distributed in the two cacao habitats as follows: five piles of rotting banana trunk slices (about 25 pieces or disks per pile); five piles of rotting pod husks, split-lengthwise, and with 30–40 husk-halves per pile; five 1 × 1 m wooden frames filled with rotting cacao leaves. The banana trunk slices, pod husks, and leaf litter were distributed around a total of fifteen tagged cacao trees in each habitat, using a random-numbers table to assign them within a larger pool of tagged trees. For each of the three censuses (March, August, and November 1984), these substrate treatments were replaced usually about two months prior to a census. A census consisted of sampling a total of 60 banana trunk slices, 75 pod husks, and 350 leaves (selecting those matted together) from each of the two habitats, and taking about the same number of items from each of the five replicates/treatment within each habitat. At the last of three censuses, I also sampled 30 arboreal rotten cacao pods from each habitat. Substrate materials were collected in large plastic bags and their contents examined at the La Lola field station.

The La Lola experimental study allowed a comparison not only of the ant



Fig. 3. La Lola cacao habitats studied. Top: "cacao forest" habitat on the property of Amos Barker. Note heavy shade and dense vegetation. Below: "Section 25" well-maintained cacao "plantation" habitat on La Lola property. Matina cacao trees are found in both habitats.



Fig. 4. Nesting substrates studied. Counterclockwise, beginning in upper left picture: wooden frame filled with cacao leaf litter; rotting trunk slices of banana trees; arboreal rotting cacao pod; pile of rotting cacao pod husks (halves).

faunas of two very different cacao habitats at the same locality, but also for microhabitat differences in terms of ant species and abundance patterns among substrates (Fig. 4). These data, in turn were compared with the arboreal pod ant data from the La Tigra locality, about 40 km to the north.

Ant voucher specimens from both studies were identified by Roy R. Snelling (Los Angeles County Museum of Natural History), and specimens are deposited both in the Los Angeles County Museum and the Milwaukee Public Museum insect collections.

RESULTS

La Tigra arboreal cacao pods.—Although 1–3 pods out of 40 at each census contained termite colonies and no ants, by far most soft, well-rotten pods supported ant colonies, generally one species per pod. With the exception of the final census (November 1984), overall ant “occupancy” levels, for all pods on each census, ranged high, namely from about 30 to 90% (Table 1). For the first three censuses, four genera and species were found in the samples, and 60% of the ant “biomass” for the entire study (29,675 ants counted) were also found at these census periods. With the exception of the final census, *Crematogaster limata palans* Forel dominated all samples. The final pod census must be viewed an

Table 1. The distribution and approximate abundance of ant colonies in arboreal rotten *Theobroma cacao* L. (Sterculiaceae) pods at "Finca La Tigra," near La Virgen, Sarapiquí District, Costa Rica (N = 40 pods collected from the same area of cacao plantations for each of seven censuses).

Approximate Colony Size and Brood Over Census Periods												
Ant Species	3-4 Dec. 1982 ("Late Rainy")			2-3 Mar. 1983 ("Dry")			7-8 Aug. 1983 ("Mid-rainy")			10-11 Nov. 1983 ("Late Rainy")		
	No. Nests**	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)
<i>Camponotus abdominalis</i> (Fabr.)	3	15-400	l, p									
<i>Crematogaster limata palans</i> Forel	6	20-450	e, l, p	5	700-1000	e, l, p	9	15-350	l, p	1	200	l, p
<i>Wasmannia auropunctata</i> (Roger)	4	110-700	l, p				8	20-500	l, p	13	20-500	e, l, p
<i>Paratrechina longicornis</i> (Latr.)	3	100-300	l, p							3	5-500	p
<i>Solenopsis tenuis</i> Mayr				6	500-1100	e, l, p						
<i>Pheidole</i> sp. 1				1	100	e						
<i>Pheidole ares</i> Forel							3	5-80	p			
<i>Monomorium floricola</i> (Jerdon)							2	1-30	-			
<i>Solenopsis</i> sp.							1	3	-			
<i>Pachycondyla villosa</i> (Fabr.)							2	1-6	p			
<i>Camponotus planatus</i> (Roger)										1	100	l, p
<i>Crematogaster curvispinosa</i> Mayr												
<i>Tapinoma ramulorum</i> Emery												
<i>Pachycondyla crenata</i> (Roger)												
<i>P. carinulata</i> (Roger)												
<i>Neostroma metopia</i> Brown												
% pods with ant colonies		16/40 = 40%			12/40 = 30%			25/40 = 62.5%			18/40 = 45.0%	
Total genera and additions ()		4 (4)			4 (+2)			4 (+2)			1 (+0)	
Total species and additions ()		4 (4)			4 (+2)			4 (+4)			1 (+1)	
Total "biomass"*		4/40			7150			6550			2678	

* Defined as the approximate total number of ants (adults and brood - e = eggs, l = larvae, p = pupae) observed.

** I assume that one nest equates with one colony.

Table 1. Continued.

Ant Species	Approximate Colony Size and Brood Over Census Periods					
	28-29 Feb. 1984 ("Dry")	3-4 Aug. 1984 ("Mid-rainy")	20 Nov. 1984 ("Late Rainy")			
	No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)
<i>Camponotus abdominalis</i> (Fabr.)	11	70-500	e, l, p	25	50-1000	e, l, p
<i>Crematogaster limata palans</i> Forel				4	5-100	e
<i>Wasmannia auropunctata</i> (Roger)						
<i>Paratrechina longicornis</i> (Latr.)	5	50-300	l, p	5	50-500	p
<i>Solenopsis tenuis</i> Mayr	1	15	l			
<i>Pheidole</i> sp. 1						
<i>Pheidole ares</i> Forel						
<i>Monomorium floricola</i> (Jerdon)						
<i>Solenopsis</i> sp.						
<i>Pachycondyla villosa</i> (Fabr.)						
<i>Camponotus planatus</i> (Roger)	2	5-20	—			
<i>Crematogaster curvispinosa</i> Mayr				1	30	e, l, p
<i>Tapinoma ramulorum</i> Emery				1	13	—
<i>Pachycondyla crenata</i> (Roger)				1	1	—
<i>P. carinulata</i> (Roger)						
<i>Neostruma metopia</i> Brown				1	150	p
% pods with ant colonies		19/40 = 47.5%			37/40 = 92.5%	1/40 = 2.5%
Total genera and additions ()		1 (+0)			2 (+1)	1 (+1)
Total species and additions ()		1 (+1)			3 (+1)	1 (+1)
Total "biomass"		1456			7551	150

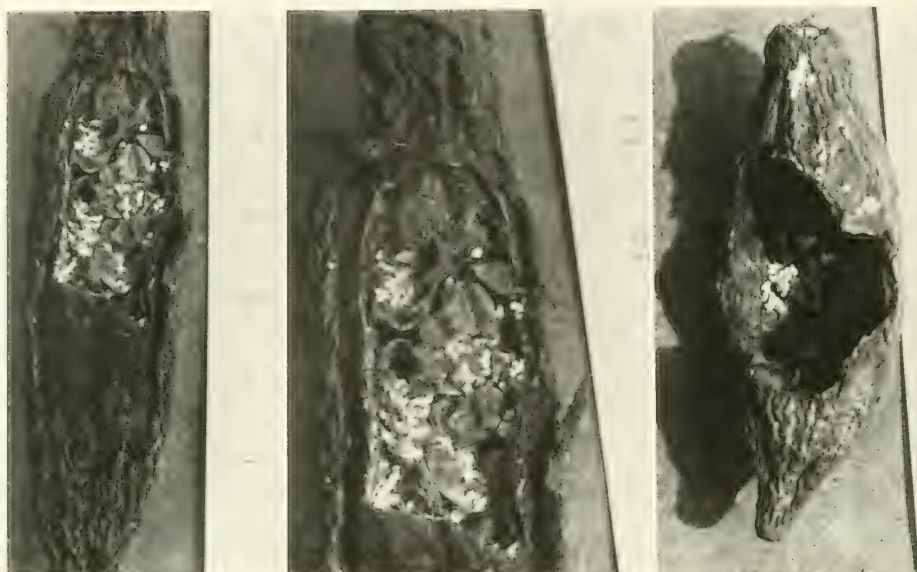


Fig. 5. Ant colonies (*Crematogaster limata palans* Forel) inside central (seed) cavities of arboreal rotting cacao pods at La Tigra. The pods have been broken open to show the colonies (with brood). Scale in mm.

anomaly, since almost all pods collected at this time were very hard and mummified due to the recent spread of the *Monilia* fungus pathogenic specifically to *Theobroma* and *Herrania* (Sterculiaceae) pods (e.g. Jorgenson, 1970). Such pods become extremely hard, precluding any colonization by insects. Ant colonies flourish inside moist, decaying pods on cacao trees, as evidenced by the majority of pods with ants also having brood (Fig. 5).

For both species number and ant biomass, I could not detect any definitive pattern between dry and rainy times of the year at La Tigra. Thus although the February 1984 census yielded the lowest ant biomass (with the exception of the November 1984 census), it also produced three species not previously collected. Furthermore, the March 1983 census, also a dry period, yielded more than five times the ant biomass as the later (February 1984) dry season census (Table 2). The observed total species richness of the arboreal pod ants at La Tigra was a product of successive censuses, as several additional genera and species were added by repeated censuses from the same cacao grove (Table 2).

Crematogaster limata palans Forel, *Wasmannia auropunctata* (Roger), *Paratrechina longicornis* (Latreille), and *Solenopsis tenuis* Mayr, were the most numerically-abundant ant species in my La Tigra samples, both in terms of colony size per census and their occurrence in successive censuses (Table 1). The relatively large (12 mm long body) ant *Camponotus abdominalis* (Fabricius) was also found within the wooden beams of the La Tigra field station. Pods with colonies of *C. abdominalis* were occasionally confined to clear plastic bags to determine when workers exited the nests: workers were not seen outside of the pods until 2000 hours (e.g. as seen on 2 March 1983).

In all cases only one ant species with brood was found inside a single cacao pod. One pod collected in August 1984 contained a four-celled nest of *Euglossa*

Table 2. Evidence for genera and species “replacement,” and associated changes in ant “biomass” with successive censuses of arboreal, rotten cacao pods at “Finca La Tigra” in northeastern Costa Rica (for N = 40 pods examined per census).

Census mo/yr	Total Genera	Total Species	New Genera	New Species	Total Ant Numbers
Dec. 1982	4	4	—	—	4140
Mar. 1983	2	2	+2	+2	7150
Aug. 1983	4	4	+2	+4	6550
Nov. 1983	1	1	0	+1	2678
Feb. 1984	1	1	0	+1	1456
Aug. 1984	2	3	+1	+3	7551
Nov. 1984	1	1	+1	+1	150
Totals	—	—	10	16	29,675

bee species within the central (seed) cavity. This pod also contained a small colony of *C. limata palans* confined to the pod wall near the petiole. *Crematogaster limata palans* colonies were found both within the pod wall tissues and central cavity of pods.

Insects, including the larval and pupal stages of Diptera, particularly Ceratopogonidae and Cecidomyiidae, were occasionally found in pods with ants, but more frequently in pods unoccupied with ant colonies. Usually 1–4 larvae and/or pupae of the ceratopogonid *Forcipomyia cinctipes* group were found in pods with *C. limata* in particular. But larval abundance of this midge increased to 20–40 per pod in pods without *C. limata* and other ants. Likewise, 1–2 larvae of Cecidomyiidae were found in pods with *C. limata*, and higher numbers in pods without ants. Midge larvae and other insects, such as at least three species of Staphylinidae, were not found within ant colonies, but generally in other portions of the same pod. Virtually all pods with ants and other insects inside them were very soft and moist, and easy to crush with gentle pressure from the fingers. These pods also were not broken, i.e. they did not have holes. In *Theobroma cacao* L. the pods do not drop from the tree when mature.

Of all ants found in the La Tigra pod samples over all seven census dates combined, 70% were *C. limata*. Of the total 128 ant colonies found in the 280 pod-sample for all dates (45.17%), 69 of these, or 53.91%, were *C. limata palans*. No ant species was found in all seven censuses, but *C. limata palans* occurred in six. *Wasmannia auropunctata* ranked second most numerous, appearing in four censuses, followed by *Solenopsis tenuis* in three, and both *C. abdominalis* and *Pheidole* sp. 1 in two. All other thirteen ant species found in this survey occurred only once (i.e. were “rare”). The genera *Crematogaster*, *Solenopsis*, *Pheidole*, *Camponotus*, and *Pachycondyla* were each represented by two species in the La Tigra arboreal cacao pod censuses.

La Lola ground-nesting studies.—A total of 19 genera and 26 species of ants were found in the “cacao forest” adjacent to La Lola, while only 12 genera and 16 species were found in the “plantation” habitat at La Lola during the same period (Tables 3 and 4). All but two species found in the cacao plantation (*Pachycondyla impressa* (Roger) and *Odontomachus crythrocephalus* (Emery) were also found in the cacao forest habitat, considering all substrates and seasons examined (Tables 3 and 4). But the cacao forest had an additional 12 species not found at

Table 3. The distribution and approximate abundance of ants in various substrates in the "cacao forest" habitat at "Finca Experimental La Lola," near Siquirres, Limon Province, Costa Rica.

Census Date	Ant Species	Numbers of Individuals (Colonies) Distributed in Various Substrates		
		Banana Trunk Slices (N = 60/census)		
		No. Nests**	Range in Colony Size	Brood (?)
7-10 March	<i>Smithistruma alberti</i> (Forel)	6	20-150	p
1984	<i>Cyphomyrmex minutus</i> Mayr	1	100	l, p
("dry")	<i>Strumigenys lanuginosa</i> Wheeler	1	75	l, p
	<i>Pachycondyla stigma</i> (Fabricius)	1	2	—
	<i>Solenopsis</i> sp. 2	2	50-100	l, p
	<i>Solenopsis</i> sp. 1	2	5-100	l, p
	<i>Solenopsis</i> sp.	2	10-60	l, p
	<i>Oligomyrmex</i> sp.	1	1	—
	<i>Gnamptogenys striatula</i> (Emery) group	2	40-150	p
	<i>Gnamptogenys striatula</i> (Emery) group	1	30	—
	<i>Hypoponera nitidula</i> (Emery)	1	40	p
	<i>Cyphomyrmex salvini</i> Forel			
	<i>Megalomyrmex silvestrii</i> Wheeler			
	<i>Cyphomyrmex minutus</i> Mayr			
	<i>Paratrechina</i> sp.			
	<i>Brachymyrmex</i> sp.			
Total genera 12				
Total species 16				
8-12 Aug.	<i>Strumigenys rogeri</i> Emery	4	20-75	e, p
1984	<i>S. elongata</i> Roger	1	20	p
("mid-rainy")	<i>Prionopelta amabilis</i> Borgmeier	1	10	—
	<i>Solenopsis</i> sp. 2	13	25-100	e, l, p
	<i>Smithistruma alberti</i> (Forel)	4	50-100	e, l, p
	<i>Wasmannia auropunctata</i> (Roger)	2	5-20	p
	<i>Hypoponera</i> sp. (<i>opacior</i> group)	1	8	l
	<i>Gnamptogenys striatula</i> (Emery) group	7	25-150	l, p, alates
	<i>Ectatomma ruidum</i> Roger	1	5	—
	<i>Hypoponera nitidula</i> (Emery)			
	<i>Cyphomyrmex salvini</i> Forel			
	<i>Cyphomyrmex minutus</i> Mayr			
	<i>Pheidole</i> sp. 15			
	<i>Paratrechina</i> sp.			
	<i>Odontomachus minutus</i> Emery			
	<i>Thaumatomyrmex paludis</i> Weber			
Total genera 14				
Total species 16				
12-16 Nov.	<i>Solenopsis</i> sp. 2	6	50-150	l, p, alates
1984	<i>Gnamptogenys striatula</i> (Emery) group	4	30-150	p
("late rainy")	<i>Neostruma zeteki</i> Brown	4	30-60	e, l, p
	<i>Pheidole</i> sp. 2	1	250	p, alates
	<i>Strumigenys elongata</i> (Roger)	1	20	l
	<i>Prionopelta amabilis</i> Borgmeier	4	10-100	e, p
	<i>Smithistruma alberti</i> (Forel)	5	70-150	e, l, p
	<i>Hypoponera nitidula</i> (Emery)	2	70-150	p
	<i>Solenopsis tenuis</i> Mayr			
	<i>Cyphomyrmex minutus</i> Mayr			
	<i>Pheidole</i> sp. 4			
Total genera 9				
Total species 11				
Overall distinct genera 19				
Overall distinct species 26				

Table 3. Extended.

Numbers of Individuals (Colonies) Distributed in Various Substrates								
Cacao Pod Husks (N = 75/census)			Leaf Litter (N = 350/census)			Arboreal Rot. Pods (N = 30/census)		
No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)
			1	20	p			
			6	10–100	p			
1	50	p	5	5–50	p			
1	10	p						
3	150–300	l, p					No Data	
1	150	p						
			2	20–30	p			
			1	40	p			
			1	40	p			
2	20–50	e	1	1	—			
2	20–40	e	7	50	e		No Data	
			5	20–30	e			
12	15–100	p, alates	6	35–100	e, p			
1	20	—						
2	15–50	p						
			1	30	e			
			1	50	e			
			1	30	e			
			1	1	—			
1	1	—						
2	30–70	l, p	5	50–60	l, p			
			1	80	l, p			
1	40	p						
1	25	p						
1	30	p				5	200–800	l, p
			1	10	l, alates	1	100	p

Table 4. The distribution and approximate abundance of ants in various substrates in the "cacao plantation" habitat at "Finca Experimental La Lola," near Siquirres, Limon Province, Costa Rica.

Census Date	Ant Species	Numbers of Individuals (Colonies) Distributed in Various Substrates		
		Banana Trunk Slices (N = 60/census)		
		No. Nests**	Range in Colony Size	Brood (?)
7-10 March	<i>Solenopsis tenuis</i> Mayr	1	50	p
1984	<i>Solenopsis</i> sp. 2	1	30	l, p
("dry")	<i>Gnamptogenys striatula</i> (Emery) group	1	30	p
	<i>Hypoponera nitidula</i> (Emery)	1	3	—
	<i>Oligomyrmex</i> sp.	8	20-100	l, p
	<i>Paratrechina</i> sp.	1	3	—
	<i>Pheidole</i> sp. 15			
	<i>Odontomachus minutus</i> Emery			
	<i>Pachycondyla impressa</i> (Roger)			
Total genera	8			
Total species	9			
8-12 Aug.	<i>Gnamptogenys striatula</i> (Emery) group	4	5-50	e
1984	<i>Strumigenys rogeri</i> Emery	2	50-100	e, p
("mid-rainy")	<i>Wasmannia auropunctata</i> (Roger)	1	50	e
	<i>Solenopsis</i> sp. 2	10	50-100	e
	<i>Smithistruma alberti</i> (Forel)	1	80	p
	<i>Prionopelta amabilis</i> Borgmeier			
	<i>Pheidole</i> sp.			
	<i>Odontomachus erythrocephalus</i> Emery			
	<i>Paratrechina</i> sp.			
Total genera	9			
Total species	9			
12-16 Nov.	<i>Solenopsis</i> sp. 2	5	25-80	l, p
1984	<i>Solenopsis</i> sp. 1	1	150	l, p
("late rainy")	<i>Gnamptogenys striatula</i> (Emery) group	2	12-25	l, p, alates
	<i>Smithistruma alberti</i> (Forel)			
	<i>Wasmannia auropunctata</i> (Roger)			
	<i>Paratrechina</i> sp.			
	<i>Hypoponera nitidula</i> (Emery)			
Total genera	6			
Total species	7			
Overall distinct genera	12			
Overall distinct species	16			

all in the plantation. Within the cacao forest, the habitat with the most diverse ant fauna, the following ant species were found at all three censuses: *Solenopsis* sp. 2, *Smithistruma alberti* (Forel), *Cyphomyrmex minutus* Mayr, and *Gnamptogenys striatula* (Emery) group (Table 3). The highest occupancy level for the rotting banana trunk slices (2 pieces occupied) was seen in the cacao forest for *Solenopsis* sp. 2 as well as in the plantation (N = 16 pieces occupied). In the cacao forest, both *S. alberti* and *G. striatula* followed closely, with N = 15 and 13 pieces occupied, respectively. For the plantation, both *G. striatula* and *Oligomyrmex* followed closely, with N = 7 and 8 pieces of trunk slices occupied, respectively. In both habitats, *Solenopsis* had the most species, namely, four in the cacao forest

Table 4. Extended.

Numbers of Individuals (Colonies) Distributed in Various Substrates								
Cacao Pod Husks (N = 75/census)			Leaf Litter (N = 350/census)			Arboreal Rot. Pods (N = 30/census)		
No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)	No. Nests	Range in Colony Size	Brood (?)
1	50	p						
1	20	l, p						
			5	40–60	p			No Data
			1	200	p, alate			
			1	1	—			
			1	1	—			
2	50	p						
1	50	e						
			1	8	—			
			5	30–60	e, l, p			
1	100	e						No Data
1	100	e						
1	20	e, l						
1	5	p						
			3	25–200	e, l, p			
2	400	l, p						
1	400	l, p	3	30–50	p			
3	50–200	l, p						
2	200–300	l, p	2	20–100	l, p			
			1	1	p (l)			

and three in the plantation. All other genera were represented by 1–2 species in the cacao forest, and by one species, with the one exception of *Pheidole* with two species, in the cacao plantation (Tables 3 and 4). There is a general indication of brood being present in both habitats for all three census periods (Tables 3 and 4). For all census dates combined, the cacao forest habitat has both the highest number of species and ant biomass as compared to the nearby plantation, and much of the ant fauna is accounted for by the rotting banana trunk slices (Table 5). For both banana trunk slices and cacao pod husks, the occupancy levels in the cacao forest were almost twice those of the plantation (Table 5). The ground leaf litter tended to have the lowest ant biomass across all census dates. Occupancy

rate for all substrate-types tends to be less than, or near, 10% across all census dates, but the highest occupancy level occurred at the mid-rainy season census in the cacao forest (Table 5). From the sample of 30 arboreal rotten cacao pods in each habitat in November, only a single pod in the cacao forest yielded an ant colony (*S. alberti*, approx. 100 ants with brood). Unlike the La Tigra census a few days later, none of these pods was hardened with the *Monilia* disease.

In terms of both species number and biomass, it is clearly the banana trunk slice "microhabitat" that supports the largest component of both the forest and plantation habitat and faunas at the La Lola locality (Table 5).

Faunal "overlap" between La Tigra and La Lola.—Twelve of the sixteen species of ants found at La Tigra in arboreal rotten cacao pods were not found at La Lola, a faunistic non-overlap of 75.00%. Furthermore, several genera of ants in the La Tigra study were not found in the La Lola samples: *Camponotus*, *Crematogaster*, *Momorium*, and *Tapinoma*. Genera in common between the two localities include: *Pheidole*, *Pachycondyla*, *Solenopsis*, *Wasmannia*, *Paratrechina*, and *Neostruma*. Two species, *W. auropunctata* and *S. tenuis*, were found at both localities. Overall, the La Tigra pods harbored many more ant colonies than the banana trunk slices and husk-halves on the ground in both La Lola habitats.

DISCUSSION

Within a habitat, the number of resident ant species, and their patterns of resource utilization, including nesting sites, is often determined by the diversity of microhabitats available (e.g. Carroll and Janzen, 1973; Cole, 1946; Haber et al., 1981; Kempf, 1972; Levings, 1983; Wilson, 1976a). My data suggest that for Costa Rican cacao habitats, the resident assemblages of ground-nesting ants is determined in part by the availability of different types of nesting substrates. There is a tendency to find different ant species when sampling a diversity of substrates (microhabitats) within a cacao habitat. Furthermore, the diversity of ground-nesting ant species tends to be greater in the "cacao forest" when compared to a well-maintained cacao plantation at the same locality. The prevailing complexity of the vegetation in an abandoned cacao habitat which is returning to forest, coupled with intense shade tending to provide very moist conditions throughout the year, may be key factors in promoting ant species richness in a cacao forest habitat in Costa Rica.

Several recent habitat studies of ants in Costa Rica suggest that a greater number of species occurs in forest habitats (e.g. Jeanne, 1979; Lieberman and Dock, 1982). A similar pattern may hold for other tropical regions as well (e.g. Cole, 1983; Leston, 1979; Levings, 1983; Wilson, 1976a). But Young (1983) found a greater number of ant species within the La Tigra cacao plantation than in an adjacent strip of mixed primary and secondary tropical rain forest, a result in direct contrast with the data presented here for La Lola. This difference may be explained, at least in part, by the differences in the cacao plantation habitats between La Tigra and La Lola. The La Tigra cacao plantation is considerably younger than La Lola, and it is characterized by a natural canopy of forest trees left behind when the understory was cleared for planting cacao trees. Furthermore, La Tigra has a brush layer of diverse herbaceous species, in direct contrast with the relatively uniform grass cover in the "Section 25" cacao grove at La Lola. Cacao plantation age,

combined with the degree to which natural vegetation occurs in the plantation, may determine in large part the ant assemblages of the plantation. A vegetationally more diverse cacao habitat may provide a greater range of resources for ant species. Presumably the cacao forest adjacent to La Lola is more resource-rich for ants, and perhaps other insects, than the La Lola plantation itself, a pattern suggested by my data. Such a contention would also support the unusual case of cacao habitats sometimes having diverse ant faunas (Young, 1983).

A greater number of ant species was found in the ground-substrate censuses at La Lola than in the rotten arboreal cacao pods at La Tigra. This is not an unexpected finding, given the greater heterogeneity and larger sample sizes of the La Lola substrates compared to the La Tigra study. What is interesting, however, is the apparently high degree of species non-overlap between the La Tigra arboreal surveys and the La Lola ground surveys. To what degree such a difference is due to unexplained differences between the two localities or due to the nature of the microhabitat stratification (i.e. arboreal versus ground-nesting/foraging) cannot be deduced from my study. Yet some ant species in the tropics are largely arboreal nesters (e.g. Hilje, 1980; Huxley, 1980; Levieux, 1975; Levieux and Louis, 1975; Swain, 1980; Wilson, 1971 and many included references). Thus it would not be surprising to discover that my observed differences between La Tigra and La Lola were due largely to an effect of vertical stratification within the cacao habitat. At La Lola, up to about 10% of the insects found on cacao foliage are ants (Andrews, 1979). Arboreally-nesting ant species in cacao may also actively forage in the cacao foliage, as suggested by ant studies in the tropics (e.g. Carroll and Janzen, 1973; Wilson, 1976b; Swain, 1980).

Several of the ant genera found ground-nesting at La Lola are well known for nesting in a range of ground-level microhabitats (e.g. Mann, 1920; Wheeler, 1906, 1911, 1913; Wheeler and Mann, 1914), even though some genera and species are found both terrestrially and arboreally for nesting sites (e.g. Kempf, 1972; Wilson, 1971). The presence of *Camponotus planatus* (Roger) in arboreal rotten cacao pods at La Tigra complements earlier observations of this ant being a stem dweller in the Guanacaste Province of Costa Rica (Carroll and Janzen, 1973). O'Dowd (1979) found that *Solenopsis* was common on ground-level honey baits while *Crematogaster* was common at arboreal honey baits. My data clearly shows a similar pattern for nesting differences between these two genera. Similarly, *Crematogaster limata*, by far the most abundant ant species discovered nesting arboreally in cacao pods at La Tigra in my study, commonly forages in vegetation in Costa Rica (Jeanne, 1979). But *Solenopsis tenuis*, nesting both arboreally and terrestrially in cacao habitats in my study, also forages primarily in vegetation in Costa Rica (Jeanne, 1979). Robert Jeanne (1979) also found that *Solenopsis* and *Pheidole* foraged primarily on the ground. Together with observations of yet other species occurring both arboreally and terrestrially in the tropics (e.g. Kempf, 1972; Wheeler and Mann, 1914), such observations suggest that some ant species are resource "generalists" in terms of utilizing both terrestrial and arboreal resources, while others are much more restricted in this sense.

My observations of a few ant species "dominating" within a habitat, in terms of colony size and the frequency of occupancy among substrate (nesting) parcels, is not unusual for tropical agricultural habitats (e.g. Adams et al., 1981; Leston, 1973, 1978; Saks and Carroll, 1980; Samways, 1981, 1983). Even though lowland

Table 5. Effects of habitat-type ("cacao forest"; "cacao plantation") and season ("dry"; "mid-rainy"; "late rainy") on the overall distribution and abundance of ant species in various substrates at "Finca Experimental La Lola," near Siquirres, Limon Province, Costa Rica.

Substrate Type and % Occupancy	Distribution of Individuals ("Biomass") and Species Among Habitats and "Seasons"							
	7-10 March 1984 ("Dry")				8-12 August 1984 ("Mid-rainy")			
	Cacao Forest		Cacao Plantation		Cacao Forest		Cacao Plantation	
	No. Individ.	No. Species	No. Individ.	No. Species	No. Individ.	No. Species	No. Individ.	No. Species
Banana trunk slices (60 + 60)*	930	11	375	6	1436	9	908	5
% Occupied	20/60 = 33.33%		13/60 = 21.67%		34/60 = 56.67%		18/60 = 30.00%	
Pod husks (75 + 75)	850	4	70	2	665	6	325	6
% Occupied	6/75 = 8.00%		2/75 = 2.67%		19/75 = 25.33%		7/75 = 9.33%	
Leaf litter (350 + 350)	548	6	510	4	1022	8	543	3
% Occupied	15/350 = 4.28%		8/350 = 2.29%		19/350 = 5.43%		9/350 = 2.57%	
Arbor, rot. pods (35 + 35)	No Data		No Data		No Data		No Data	
% Occupied								
Diseased pods on ground (35 + 35)	No Data		No Data		No Data		No Data	
% Occupied								
Totals across substrates	2328		955		3123		1776	
Overall % occupancy	41/485 = 8.45%		23/485 = 4.74%		72/485 = 14.85%		34/485 = 7.01%	

* Numbers in parentheses refer to the number of substrate pieces sampled in each of the two cacao habitats.

Table 5. Continued.

Substrate Type and % Occupancy	Distribution of Individuals ("Biomass") and Species among Habitats and "Seasons"									
	12-16 November 1984 ("Late Rainy")				Total Cacao Forest		Total Cacao Plantation		Overall Total Combined Habitats	
	Cacao Forest		Cacao Plantation		Cacao Forest		Cacao Plantation		Cacao Forest	
	No. Individ.	No. Species	No. Individ.	No. Species	No. Individ.	No. Species	No. Individ.	No. Species	No. Individ.	No. Species
Banana trunk slices (60 + 60)*	2265	8	477	3	4631		1760		6391	
% Occupied	27/60 = 45.00%		8/60 = 13.33%		81/180 = 45.00%		39/180 = 21.67%		120/360 = 33.33%	
Pod husks (75 + 75)	195	4	2050	4	1710		2445		4155	
% Occupied	5/75 = 6.67%		8/75 = 10.67%		30/225 = 13.33%		17/285 = 7.56%		47/450 = 10.44%	
Leaf litter (350 + 350)	480	3	231	3	2050		1284		3334	
% Occupied	7/350 = 2.00%		6/350 = 1.71%		41/1050 = 3.90%		23/1050 = 2.19%		64/2100 = 3.05%	
Arbor. rot. pods (35 + 35)	3300	2	0	0	—		—		—	
% Occupied	6/35 = 17.14%		0.00%		—		—		—	
Diseased pods on ground (35 + 35)	0	0	100	1	—		—		—	
% Occupied	0.00%		1/35 = 2.85%		—		—		—	
Totals across substrates	6240		2858		8391		5489		13,880	
Overall % occupancy	45/485 = 9.28%		23/520 = 4.42%		152/1455 = 10.45%		79/1455 = 5.43%		231/2910 = 7.94%	

tropical rain forest sites are expected to be very rich in ant species (e.g. Ayre, 1977; Evans, 1982; Kempf, 1974, 1975; Levings, 1983; Levings and Franks, 1982) and for insects in general (e.g. Amendegnato and Descamps, 1980; Hanski, 1980) cacao and other lowland agricultural habitats tend to have less diverse ant faunas characterized by specific "assemblages" of species (e.g. Bigger, 1981; Jackson, 1984; Leston, 1973, 1978, 1979). Genera such as *Crematogaster*, *Pheidole*, and *Solenopsis* dominate such assemblages in cacao and other tropical crop habitats throughout the world (e.g. Samways, 1981, 1983).

There is some evidence that ants prefer nesting in the most shaded patches within a cacao habitat (e.g. Ackonor, 1981, 1983; Leston, 1973). Both ground-level and arboreally-active insects in lowland tropical forests may exhibit fluctuations in both abundance and overall species richness in direct response to tropical seasonality (e.g. Baker, 1976; Fisk, 1982; Levings, 1983). Ant species in cacao habitats may preferentially seek well-shaded nesting microhabitats as a means to "buffer" the impact of the tropical dry season, even in localities where seasonal cycles of rainfall are less pronounced. My data did not reveal any definitive patterns of seasonal changes in the structure of ant assemblages in cacao habitats, possibly because my censuses were too widely-scattered, and my sample sizes at each census, relatively small. The maintenance of a shade cover throughout much of the year in the La Lola cacao forest may be a major influence upon the overall observed high species richness of ants found there. Naturally-rotting arboreal cacao pods provide a very moist nesting microhabitat off the ground. Healthy pods, gouged out by vertebrates seeking the sweet-tasting pulp of cacao seeds, very seldom become colonized by ants once they rot. Intact, unbroken pods are frequently colonized by a diverse ant fauna, as shown here. Furthermore, halved pod husks on the ground are not as suitable as nesting microhabitats as are rotting banana trunk slices. In terms of overall attractiveness as nesting sites for diverse assemblages of ant species, the ground-level banana trunk slice replaces the intact rotted arboreal cacao pod as a frequently colonized resource in cacao habitats in Costa Rica. Such observations suggest that microhabitat "attractiveness" for tropical ant nesting is governed largely by physical parameters (i.e. moisture-retention and darkness) rather than intrinsic chemical attractiveness of well-rotted plant tissues (i.e. cacao pod walls versus banana trunk slices).

About 20% of the forest foliage insects in a tropical forest habitat, in the understory, can be ants, contrasted with about half this frequency for cacao habitats (Andrews, 1979). In some instances, however, open canopy habitats may promote species-rich ant assemblages in the tropics (e.g. Jeanne, 1979 and see also Thompson, 1981 for general discussion).

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NOTE

The Hickory Aphid, *Protopterocallis fumipennella* (Fitch) and its Junior Synonym, *P. canadensis* Richards, New Synonymy (Homoptera: Aphididae)

The identity of *Aphis fumipennella* Fitch has always been problematical. Bissell (1932. *Ann. Entomol. Soc. Am.* 25: 730–735) thought the type specimen too broken for full identification. Smith and Parron (1978. *North Carolina Agric. Exp. Sta. Tech. Bull.* 255: 1–428) quoted from my correspondence and listed it as “*Protopterocallis* ? *fumipennella* (Fitch) nomen dubium,” adding 12 state records, evidently based on the determinations of *Myzocallis fumipennellus* (Fitch), a misidentification for the black pecan aphid. I believe these entries are largely in error. Knowlton (1983. *Utah Agric. Exp. Sta. Bull.* 509: 1–199) listed *P. fumipennella* on pecan at St. George, Utah; this is definitely an error for *Melanocallis caryaefoliae* (Davis).

In my earlier report on the type specimen (Bissell, 1932. *Ibid.*) I included the primary sensorium with the unguis in my measurements; however, when included with the base, antennal segment 6 is 0.143 plus 0.045, that is, base three times as long as unguis. Another character in common between *fumipennella* and *canadensis* (below) is the presence of three small tubercles on the posterior margin of the head, dorsally.

Richards (1965. *Entomol. Soc. Can. Mem.* 44: 1–149) erected *Protopterocallis* for a new species, *P. canadensis* Richards. Bissell (1978. *Maryland Agric. Exp. Sta. Misc. Publ.* 911: 1–78) gave additional information on the genus. Since that time I have reexamined the type of *fumipennella* as well as additional specimens from the type locality, Salem, New York and cannot find morphological differences between *fumipennella* and *canadensis*. I therefore declare them synonyms. This species has been most common on *Carya cordiformis* Wang (K. Koch) but has also been taken on *C. glabra* (Mill.) Sweet, *C. ovata* (Mill.) K. Koch and *C. tomentosa* (Poir.) Nutt., but not on pecan, *C. illinoensis* (Wang.) K. Koch.

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THE GENUS *PACHODYNERUS* IN NORTH AMERICA
(HYMENOPTERA: VESPIDAE: EUMENINAE)

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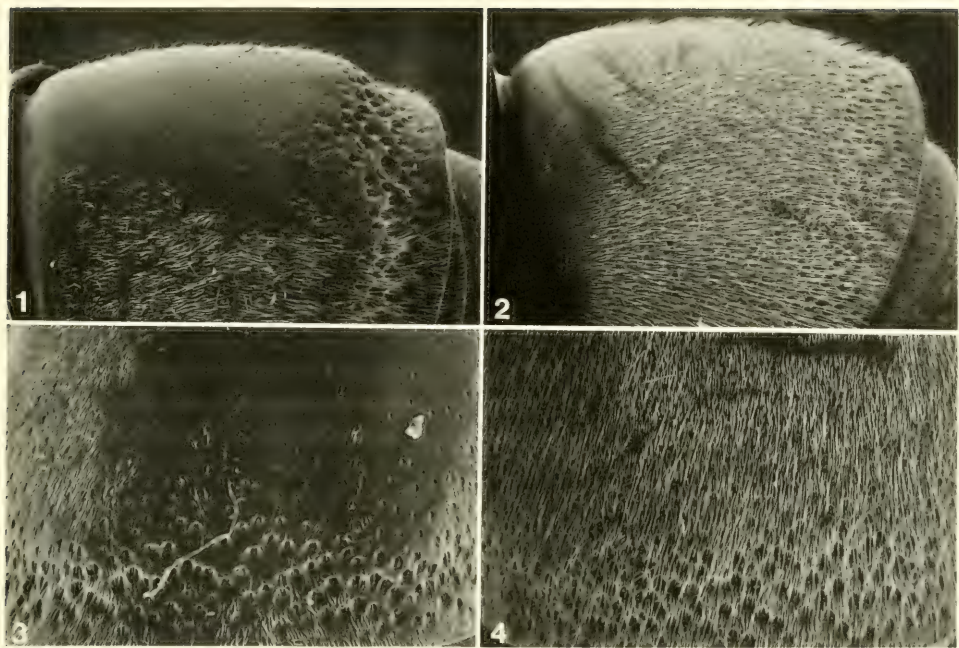
Abstract.—The five species of *Pachodynerus* in North America are keyed and notes on their biology and distribution presented. The five species are: *acuticarinatus* (Cameron), *californicus* (Saussure), *erynnis* (Lepeletier), *nasidens* (Latreille) and *praecox* (Saussure).

Pachodynerus is a potter wasp genus common from Argentina to the southern United States, and also adventive in Hawaii and Micronesia. Carpenter and Cumming (1985) established that it is a monophyletic group most closely related to the *annulatus* species-group of the genus *Euodynerus*. The genus has not been revised since Saussure (1875), and although some partial keys have been published (Zavattari, 1912; Brèthes, 1920; Bequaert, 1948), no key to the Nearctic species has been available. Recent treatments of these species (Krombein, 1979; Smith, 1984) incorrectly apply some names. In this paper I call attention to the correct nomenclature and present a key to the five species found in North America (including Central America), together with notes on their behavior and distribution.

Bohart (1951) listed four species from the United States, three of which also occur in Mexico. These were *acuticarinatus* (Cameron) (Arizona, Texas and Mexico), *erynnis* (Lepeletier) (southeastern United States from South Carolina to Louisiana), *nasidens* (Latreille) (Arizona and Texas south to Central America, the Caribbean and Hawaii; also occurring in Florida, throughout South America, and introduced on numerous islands throughout Micronesia) and *pulverulentus* (Viereck) (California, Arizona and Lower California). Bohart (1965) synonymized *acuticarinatus* and *pulverulentus* with *astraeus* (Cameron), and this nomenclature was followed by Krombein (1979) and Smith (1984). However, Willink (1972) considered *acuticarinatus* a valid species and synonymized *astraeus* and *pulverulentus* with *praecox* (Saussure), a species widespread throughout South America. I agree with this treatment, and outline the synonymy and distribution below. Acronyms for collections are those of Heppner and Lamas (1982).

KEY TO NEARCTIC SPECIES OF *PACHODYNERUS*

1. Maculations mostly dull red *erynnis* (Lepeletier)
- Maculations pale or deep yellow 2
2. Tergum I with apical yellow band and brownish, nearly translucent border posterior to this 3



Figs. 1–4. Tergum II of *Pachodynerus* spp. 1, *P. acuticarinatus*, lateral view. 2, *P. nasidens*, lateral view. 3, *P. acuticarinatus*, dorsal view. 4, *P. nasidens*, dorsal view.

- Tergum I completely dark, without yellow and nearly translucent border (a dark brown border occasionally present) 4
- 3. Propodeum with dorsal lamellae; terga I and II strongly punctured *praecox* (Saussure)
- Propodeum smooth dorsally, without lamellae; terga I and II scarcely punctured *californicus* (Saussure)
- 4. Coarse punctation of tergum II confined to narrow apical zone (Figs. 1, 3); scutal pubescence silvery-yellow, sparse *acuticarinatus* (Cameron)
- Punctation of tergum II fine or coarse, but only gradually decreasing in density anterior to apex (Figs. 2, 4); scutal pubescence golden-yellow and very dense *nasidens* (Latreille)

Pachodynerus acuticarinatus (Cameron)

Odynerus acuticarinatus Cameron, 1909: 82, type ♀ (BMNH)—“Nogales, Arizona.”

I have seen the type in the British Museum, and agree with Willink (1972) that it is a distinct species. It is readily distinguished from *praecox* by the absence of an apical yellow band and nearly translucent border on tergum I (a few specimens have a dark brown border). However, it is very similar to *nasidens*, and some specimens of the latter (particularly males) show a more or less distinct posterior zone of coarser punctation on tergum II. However, the punctures are denser and more regularly spaced in *nasidens* (cf. Figs. 1, 2), and the difference in the color and density of scutal pubescence is still helpful in distinguishing the two species.

The male clypeus also differs in the two species: in *acuticarinatus* the apical emargination is about as wide as the distance between the emargination and the mandibular condyle; in *nasidens* it is usually $0.8\times$ as wide as this distance. Thus, the clypeus of *nasidens* projects more strongly apically.

Besides the type, I have seen specimens of *acuticarinatus* from TEXAS: Hidalgo Co., Bentsen-Rio Grande State Park, and Cameron Co., Southmost Ranch (both USNM) and Brownsville (MCZ and USNM); ARIZONA: Sabino Canyon, Santa Catalina Mts.; and Palmerlee (MCZ); Cochise Co., Dragoon (MCZ), San Bernardino Ranch (USNM), Canelo, and Huachuca Mts., Miller Canyon (both CU); Sta. Cruz Co., Ruby, and Baboquivari Mts., Brown Canyon (both USNM); Pima Co., Tucson; Sta. Rita Mts., 35 mi S. Tucson and Madera Canyon (all USNM); 13 mi ESE Continental (CU); and Texas Pass (CU); MEXICO: Jalisco, Guadalajara (MCZ and USNM); Morelos, 30–40 km NE Cuernavaca (MCZ); Puebla, Tehuacan and Jalisco, San Juan Lagos (both CU); Durango, Nombre de Dios; Tamaulipas, Victoria; Vera Cruz; and Guerrero, Chilpancingo (all USNM).

This species nests in pre-existing holes of various kinds. Rau (1940) described its nesting habits in Jacala, Tamaulipas. It was found in old cells of *Sceliphron*, which in some cases were subdivided by mud partitions. Davis (1964) reported nests in larval bagworm cases from Arizona, and there is a specimen in the USNM from Brownsville labelled “nesting in psychid bag.” Another specimen in the USNM is labelled “Reared from mud nest Sept. 18 1931 by L.P.W.” Parker and Bohart (1966) have recorded it from Arizona nesting in holes in wood.

Pachodynerus californicus (Saussure)

Odynerus californicus Saussure, 1870: 57, ♀ (MHNG)—“California.”

Odynerus saussurei Fox, 1893: 13, ♀ (lectotype CAS, no. 260, designated by Bohart, 1948: 323)—“Lower California: San Jose del Cabo.”

Odynerus recoctus Schulz, 1906: 219 (replacement name for *Odynerus saussurei* Fox, 1893, *non* André, 1884).

Saussure (1875) recorded this species from both Lower and Southern California, but Bohart (1948) described it as “apparently endemic” to Lower California. Smith (1984) recorded it from Riverside Co., Deep Canyon and termed this the first United States record, but it seems probable that Saussure’s (1875) statement noting it from Southern California was in fact correct.

Pachodynerus erynnis (Lepeletier)

Odynerus erynnis Lepeletier, 1841: 645, ♀ (MNHP).

This distinctive species is endemic to southeastern United States. It was recorded by Krombein (1958) from Cape Cod, Massachusetts, after a storm (Krombein, 1979). The biology was studied by Ashmead (1894) and Krombein (1967). It nests in pre-existing cavities such as abandoned insect burrows in wood and old cynipid galls.

Pachodynerus nasidens (Latreille)

Odynerus nasidens Latreille, 1817: 112, ♀ (MNHP?).

Odynerus simplicicornis Saussure, 1855: 253, ♂ (MNHP)—“L’île de Cuba.”

Odynerus auratus Saussure, 1858: 166, ♀ (?)—“Le Mexique.”

Odynerus nasidens var. *minor* Saussure, 1875: 233 ♂ ♀ (MHNG?)—"Mexico."
Odynerus magdalenae Kriechbaumer, 1900: 98, 105, ♀ (ZSBS)—"Columbien:
 Puerto Berrio am R. Magdalena."
Odynerus clavilinus Cameron, 1912: 222, ♀ (BMNH)—"British Guiana."

This most widespread member of the genus is found throughout the Neotropics, and is morphologically quite variable. The punctation of some Mexican specimens is similar to that of *acuticarinatus*, and a dark brown border is occasionally present. It reaches the United States in Texas and Arizona, and is also found in Florida, where it is possibly introduced (in the USNM there is a specimen from the Miami Airport, labelled as from San Jose via Belize). It is adventive on many islands in Micronesia and Hawaii. In the United States, I have seen specimens from FLORIDA: Plantation Key (USNM); Miami (MCZ) and S. Miami (CU); Monroe Co., Happy Jack Key (MCZ) and Pinellas Co., St. Petersburg (CU); and TEXAS: Weslaco (MCZ) and Laguna Madre 25 mi SE Harlingen (USNM).

The biology of *nasidens* has been the subject of numerous studies. It is well known to nest in pre-existing cavities, and the ecology of populations nesting in old *Sceliphron* cells and trap-nests in Jamaica has been investigated in detail (Freeman and Jayasingh, 1975a, b; Jayasingh, 1980; Jayasingh and Taffe, 1982). But several reports have described nests of mud cells attached to plants (Bertoni, 1911; Strand, 1912: pl. 10, fig. 13) or other surfaces. I have seen specimens at the USNM pinned with mud nests from Panama and Costa Rica, and the latter included a reared adult. This evidence should allay the doubt expressed by Krombein (1979) regarding this type of nesting behavior in *Pachodynerus*. In addition, I have collected this species constructing and nesting in burrows in the ground in both Suriname (Saramacca Dist., Raleigh Vallen-Voltzberg Natuureservaat, January 1982) and Venezuela (Guarico, Hato Masaguaral, May 1985). The capacity for completely different types of nesting behavior occurs in other eumenine species (e.g. *Ancistrocerus spilogaster* may either use pre-existing cavities or build nests of mud cells, see Krombein, 1979) but this extreme plasticity is remarkable.

Pachodynerus praecox (Saussure)

Odynerus praecox Saussure, 1855: 254, ♀ (MNHP)—"L'Amérique du Sud depuis l'Uruguay jusqu'aux missions."
Odynerus zonatus Saussure, 1870: 57, ♂ (MHNG)—"Cayenna."
Odynerus astraes Cameron, 1905: 390, ♀ ♂ (♀ BMNH)—"Mexico."
Pachodynerus validus Brèthes, 1906: 343, ♀ (MBR)—"Argentina: Jujuy."
Odynerus pulverulentus Viereck, 1908: 406, ♀ (*pulverulenta*; SMEK)—"Bill Williams's Fork, Arizona."
Odynerus clavilinus Cameron, 1912: 222, ♂ (BMNH)—"British Guiana."

The synonymy was established by Willink (1972); however, he did not list *pulverulentus*. Bohart (1965) synonymized the latter with *astraes*, and I have seen Viereck's type and consider it to be *praecox*. I have seen Cameron's types in the British Museum and concur with Willink regarding them. It occurs from the United States south to Argentina, but not in the West Indies (Menke, 1986, cites it from Trinidad and discusses relationship with the similar species *guadulpensis*). Most specimens throughout the range can be separated from *nasidens* by the characteristic apical yellow band and nearly translucent border of tergum

I, but I have seen specimens from Texas (USNM) in which these are greatly reduced medially, with the band narrow and irregular.

I have seen specimens of *praecox* from TEXAS: Cameron Co., Brownsville (MCZ and USNM); and Southmost Ranch (USNM); Hidalgo Co. (USNM); ARIZONA: Yuma (USNM and CU), Tempe (MCZ), and Phoenix (CU); and CALIFORNIA: Imperial Co. (USNM); Riverside Co., Mecca, Blythe, Coachella Valley, and Salton Sea (MCZ); Palm Canon, Colorado Desert; Needles and El Centro (all CU).

The nesting behavior of this species is also diverse. Strand (1912) mentions a nest of mud cells from Paraguay, and it has been taken in trap-nests in the United States (Parker and Bohart, 1966; Krombein, 1967; the latter paper possibly confuses this species with *acuticarinatus*).

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**LARVAL DESCRIPTION OF *RIVELLIA PALLIDA*
(DIPTERA: PLATYSTOMATIDAE), A CONSUMER OF THE
NITROGEN-FIXING ROOT NODULES OF HOG-PEANUT,
AMPHICARPA BRACTEATA (LEGUMINOSAE)**

CLAUDETTE M. BIBRO AND B. A. FOOTE

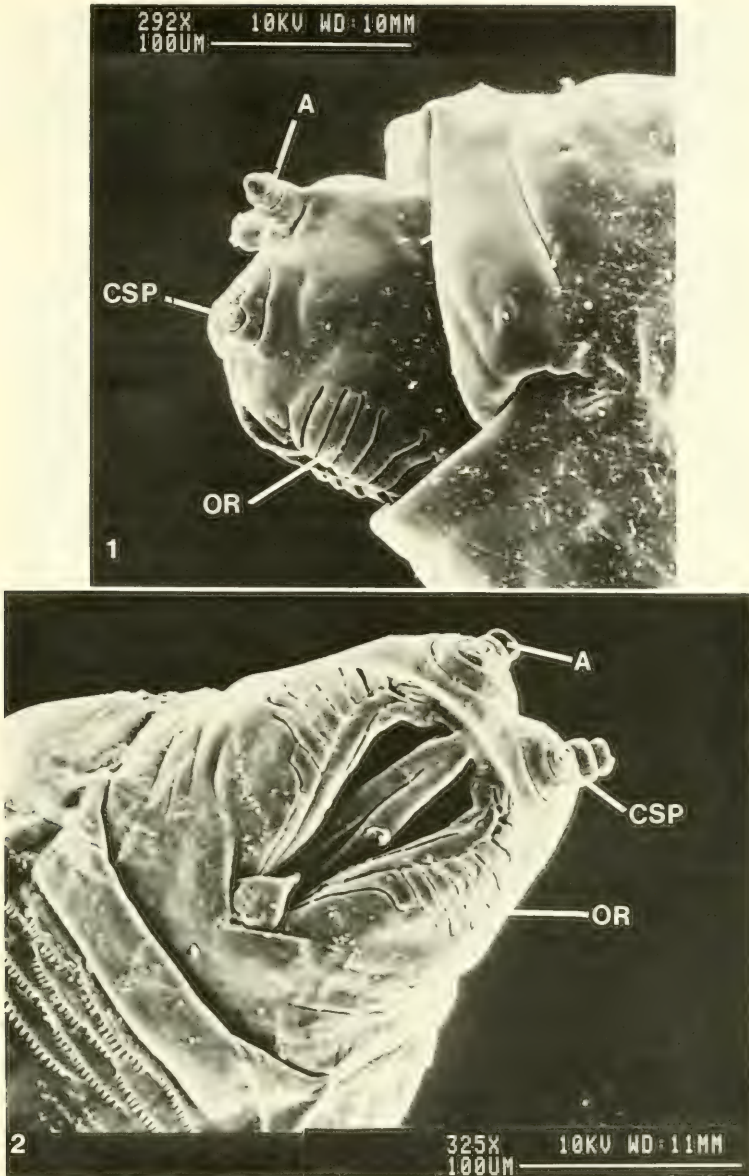
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Abstract.—The mature larva of *Rivellia pallida* Loew, a consumer of the nitrogen-fixing root nodules of hog-peanut, is described and illustrated utilizing a scanning electron microscope. A morphological comparison of four species of *Rivellia* indicates that the number of papillae bordering the anterior spiracles is of some value in distinguishing among species.

Surprisingly little biological information is available for the numerous species of acalyptrate Diptera belonging to the largely tropical family Platystomatidae. Larvae of a few species of the genus *Rivellia* are known to feed on the nitrogen-fixing root nodules of legumes (Foote, 1985), and it appears that certain of these species have shifted to agriculturally important species of Leguminosae (Diatloff, 1965; Koizumi, 1957; Seeger and Maldague, 1960) in other regions of the world. Recently, Eastman and Wuensche (1977) have elucidated the life cycle and briefly described the immature stages of *Rivellia quadrifasciata* (Macquart), a Nearctic species which is acquiring some significance as a pest of soybean, *Glycine max* L. (Newsom et al., 1978) and southern pea, *Vigna unguiculata* (L.) Walp. (Koethe and Van Duyn, 1984) in southeastern United States. Because of the probability that additional species of *Rivellia* will shift to introduced, economically significant legumes, it is important that the larval morphology and basic biology of the native North American species be described. This paper supplements the publication by Foote (1985) that presented life history data and described the larval feeding habits of *Rivellia pallida* Loew, a common and widespread woodland species that attacks the nitrogen-fixing root nodules of hog-peanut, *Amphicarpa bracteata* (L.) Fernald. Here, we utilize a scanning electron microscope to describe the mature larva of that species.

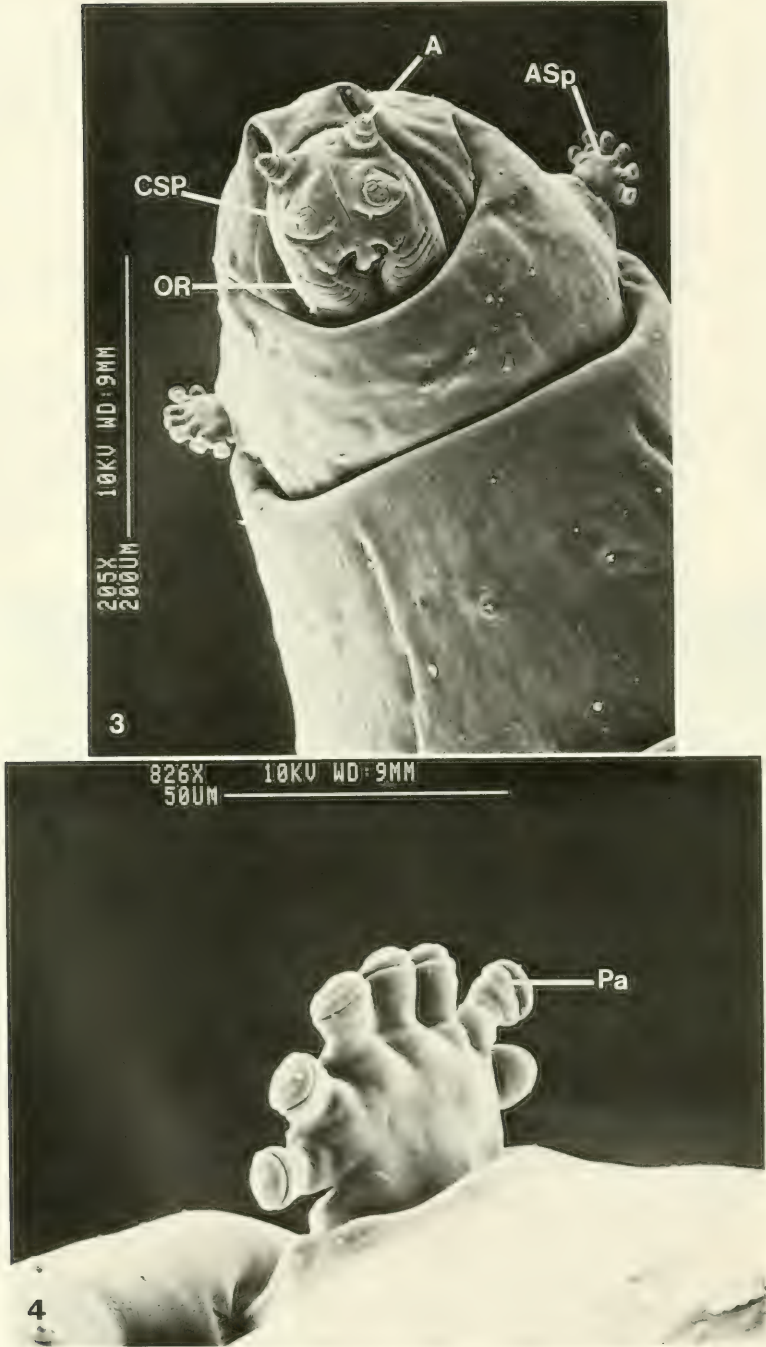
MATERIALS AND METHODS

Mature larvae were obtained from soil below stands of hog-peanut occurring in wooded habitats near the city of Kent in Portage County, Ohio. They were prepared for scanning by subjecting them to critical point desiccation, using the method of Grodowitz et al. (1982) as a guide. Larvae were killed in boiling water, placed in Supper Skipper for 30 to 60 seconds, and then transferred to Carl's Solution where they were left for approximately 24 hours. Specimens were then dehydrated in a standard ethanol series. Following these initial preparations,

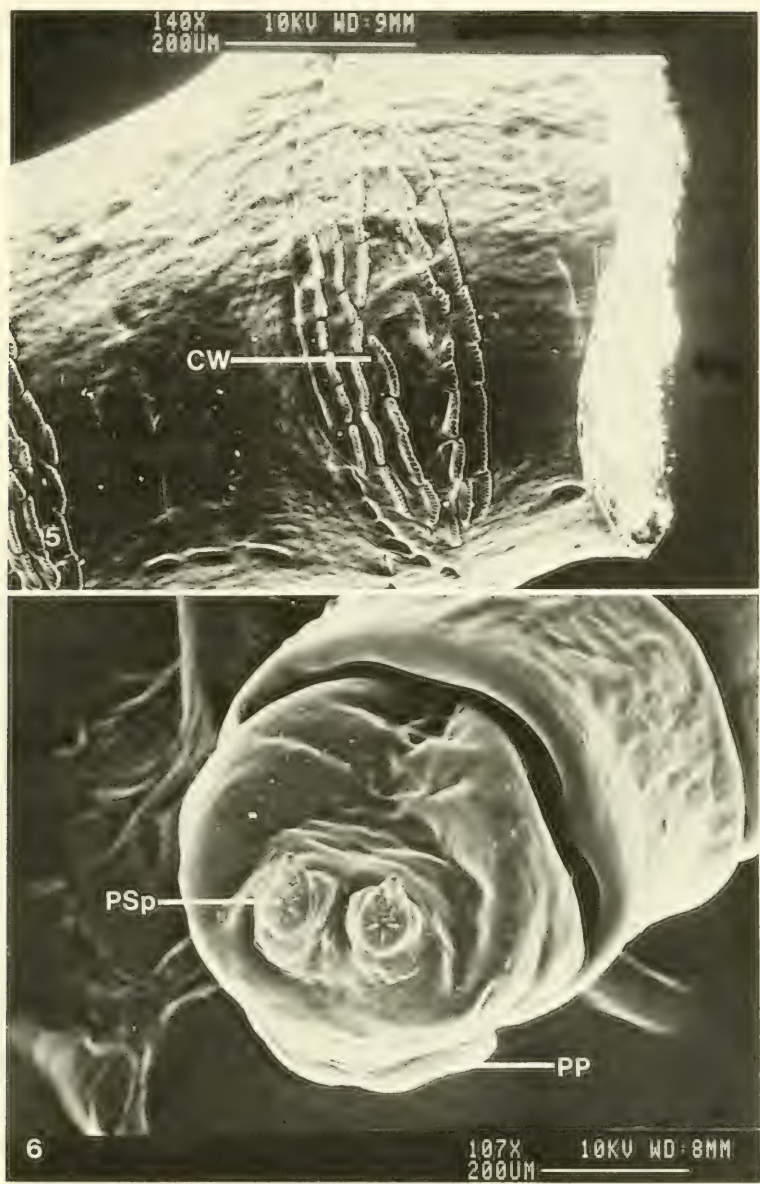


Figs. 1, 2. *Rivellia pallida*. 1, Lateral view of cephalic segment. 2, Facial mask. (A, antenna; CSP, circular sensory plate; OR, oral ridge.)

larvae were cut in desired ways so that they could be easily mounted after critical point desiccation was completed. We used the Polaron Critical Point Drying Apparatus, with ethanol as the transfer liquid and CO₂ as the transition liquid. Specimens were sputter coated with gold/palladium to a thickness of about 400 nm. Coated larvae were then examined with a Cambridge Stereoscan 100 Electron Microscope. Photographs were obtained with a high resolution camera and Polaroid (#52) film.

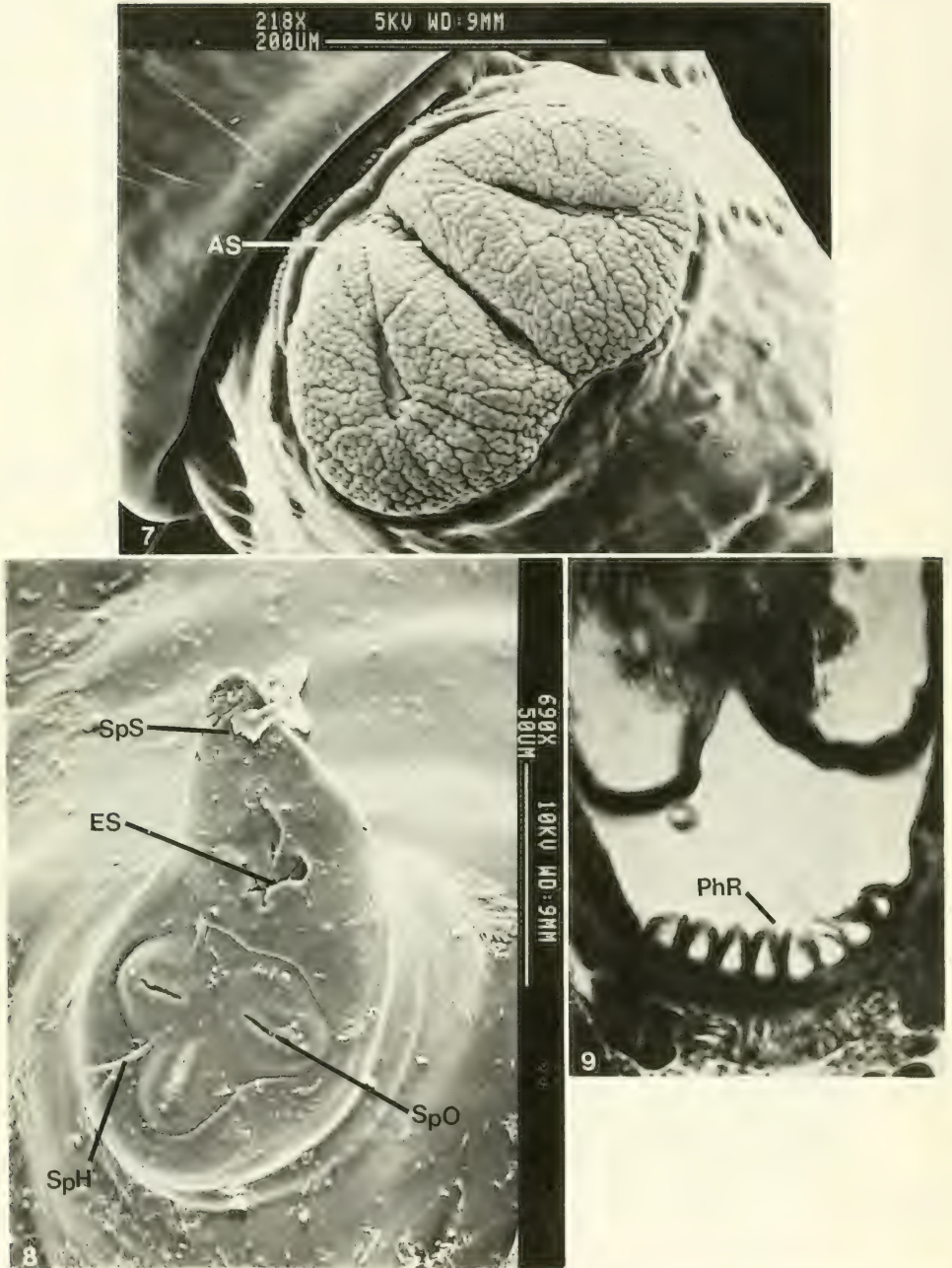


Figs. 3, 4. *Rivellia pallida*. 3, Ventral view of anterior end. 4, Anterior spiracle. (A, antenna; ASp, anterior spiracle; CSP, circular sensory plate; OR, oral ridge; Pa, papilla.)



Figs. 5, 6. *Rivellia pallida*. 5, Ventral view of fifth abdominal segment. 6, Posterior view of caudal segment. (CW, creeping welt; PP, perianal pad; PSp, posterior spiracle.)

In the examination of the *Rivellia* larval anatomy, certain surface structures of interest were studied. These included the facial mask, anterior and posterior spiracles, perianal pad, and ventral creeping welts. The cephalopharyngeal skeleton and its component sclerites were examined by light microscopy. The skeleton was dissected from the mature larva, macerated in a 10% KOH solution, and mounted in glycerol for microscopic examination.



Figs. 7-9. *Rivellia pallida*. 7, Perianal pad. 8, Posterior spiracle. 9, Cross-sectional view of filtering mechanism in floor of tentropharyngeal sclerite. (AS, anal slit; ES, ecdysial scar; PhR, pharyngeal ridge; SpH, spiracular hair; SpO, spiracular opening; SpS, spiracular spine.)

DESCRIPTION OF MATURE LARVA OF *RIVELLIA PALLIDA*

Length 5.0–8.0 mm; muscidiform, with anterior end tapering and caudal segment bluntly rounded. Integument smooth, without setae or segment-encircling spinule bands, creeping welts present ventrally. Whitish to pale yellow.

Cephalic segment (Fig. 1) retractile and bearing 2 pairs of sensory organs, 2-segmented, elongated antennae apically and circular sensory plates apicovertrally. Facial mask (Fig. 2) with 7 broad oral ridges and 8 narrow grooves leading into preoral cavity, cavity appearing to be divided by median rod and bearing triangular fleshy projection posteriorly.

Cephalopharyngeal skeleton deeply pigmented; tentoropharyngeal and hypopharyngeal sclerites separate. Dorsal cornua of tentoropharyngeal sclerite slender, connected anteriorly by narrow, weakly pigmented, somewhat fenestrated dorsal bridge; ventral cornua with small lobe dorsobasally, without windows distally; pharyngeal filtering mechanism present in floor of sclerite (Fig. 9). Hypopharyngeal sclerite H-shaped with single broad, weakly pigmented transverse bridge; parastomal bars short, rod-like, and free apically. No well-defined epipharyngeal or labial sclerites. Mandibles deeply pigmented; hook part weakly decurved, bluntly rounded apically, and lacking accessory teeth along ventral margin; basal part subrectangular, without windows; dental sclerites absent or vestigial; no accessory oral sclerites.

Thoracic segments cylindrical, without encircling spinule bands; metathorax ventrally with weakly developed creeping welt of pale spinules near posterior border of segment. Anterior spiracles borne posterolaterally on prothorax (Fig. 3); spiracles (Fig. 4) fan-shaped with 6–7 blunt papillae arranged in single row along distal margin. Abdominal segments all very similar, cylindrical, without encircling spinule bands; each segment ventrally with weak creeping welt (Fig. 5) composed of 4–5 rows of blunt-tipped, posteriorly directed spinules. Caudal segment (Fig. 6) truncate to bluntly rounded, without fleshy protuberances laterally; perianal pad (Fig. 7) bilobed, each lobe somewhat hemispherical in shape, fleshy, and reticulate, without noticeable spinule patches, but with single spinule row posterior to pad.

Posterior spiracular disc (Fig. 6) without tubercles. Posterior spiracles borne on upper half of disc, distinctly separated, and somewhat elevated on deeply pigmented bases. Each spiracular plate (Fig. 8) with dorsally or dorsolaterally projecting spine on upper surface and 3 oval to elongate-oval spiracular openings arranged ray-like around ecdysial scar, openings nearly at right angles to each other; spiracular hairs vestigial or absent.

DISCUSSION

Unfortunately, there appears to be relatively little morphological variation among larvae of different species of *Rivellia*. Larvae of four species were examined: *R. pallida*, *R. steyskali* Namba from tick trefoil (*Desmodium paniculatum* (L.) DC.), *R. viridulans* Robineau-Desvoidy from black locust (*Robinia pseudo-acacia* L.), and *R. winifredae* Namba, from groundnut (*Apios americana* Medic.). The only character that varied among the four species was the number of papillae on the distal margin of the anterior spiracles. *Rivellia pallida* and *viridulans* both possessed 6–7 papillae; *steyskali*, 7–9; and *winifredae*, 9–10. Because the number of

papillae overlapped among the four taxa, the number alone is not sufficient to distinguish species. Obviously, a much more extensive study of the larval morphology of the Nearctic species must be made before a meaningful key to the larvae can be composed.

ACKNOWLEDGMENTS

We are indebted to A. K. Graham, Kent State University, for his aid with the scanning electron microscope. We also wish to thank J. Gilliam and J. Killius at the Northeastern Ohio Universities College of Medicine for their help in critical point desiccation.

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**A NEW GENUS AND SPECIES OF WATER SCAVENGER BEETLE,
GUYANOBIUS ADOCETUS, FROM GUYANA AND ITS LARVA
(COLEOPTERA: HYDROPHILIDAE: HYDROBIINAE)**

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Abstract.—The adult of this new genus and species is described, illustrated with line drawings and scanning electron micrographs, and distinguished from related hydrobiine genera. The larva also is described, illustrated with line drawings, and distinguished from other hydrophilid larvae. The habitat of this species in the Takutu Mountains of Guyana is described.

The water scavenger beetle described here was collected during an Earthwatch expedition to the Takutu Mountains of Guyana in November–December 1983. The purpose of the fieldwork was to survey the insects of an area from which lumber was beginning to be selectively harvested. We also found that some small gold mining operations were underway in the same area. Consequently, siltation from road building, logging, and the mining operations had already caused some minor disturbances of the aquatic habitats but major portions remained undisturbed and numerous new taxa, including the one described below, were collected from them.

This new genus exemplifies the problem one finds in placing some new genera of hydrophilids in the proper subfamily and illustrates the value of using larval characteristics to help with assignments to higher categories. The habitus of the adult at first suggested an unusually large species of *Chaetarthria*, a new genus belonging to the subfamily Chaetarthriinae, perhaps related to *Chaetarthria* by its shape and similarity of habitat, or a small *Hydrobius* in the subfamily Hydrobiinae. When an attempt is made to key the adult to subfamily in the two keys now available for that purpose (d'Orchymont, 1942; Crowson, 1955), one finds that this beetle has some character states of both the Chaetarthriinae and Hydrobiinae.

Although this new hydrophilid superficially resembles the genus *Chaetarthria* by its strongly convex shape and the common excavation of the first two abdominal sterna, it differs as follows. (1) The elytra lack sutural striae. (2) The clypeus is broadly expanded and hides the thin, broad, truncate labrum. (3) The anterior margin of the first abdominal sternum has a few, fine, short setae instead of the long, dense, stout setae which extend over the excavations to the third sternum on *Chaetarthria*. (4) It is much larger in size than previously described species of *Chaetarthria*.

The small stream habitat was appropriate for either *Chaetarthria* or *Hydrobius*; but the presence of the beetles in leaf packs suggested *Hydrobius* instead of the normally psammophilous *Chaetarthria*.

The larva of this new genus is distinctly different from that of *Chaetarthria*; it keys readily to the Hydrobiinae in Bertrand's (1972) key to hydrophilid larvae and agrees well with Crowson's (1955) characterization of hydrobiine larvae. The larva of this new genus differs from that of *Chaetarthria* as follows. (1) Mandibles each with 3 teeth instead of 2 on inner edge. (2) Legs normally developed; tarsal claw present. (3) Ligula elongate, without proximal triangular plate and without a distal subcircular soft disc. (4) Labroclypeus with 5 large teeth instead of 3 teeth (1 large and 2 small).

Because of the differences between the adults and the convincing evidence the larva provides, this genus is here assigned to the Hydrobiinae.

Guyanobius Spangler, NEW GENUS

Body form hemispherical (Figs. 1–4). Length, 3.1 to 3.5 mm. Hypomera and epipleura vertical, extending well below sterna. Clypeus expanded anteriorly and laterally and conceals labrum; lateral margins extending deeply into eyes and narrowly separated from posterolateral margin of eyes (Figs. 2, 3). Antenna, 9 segmented (Fig. 10). Mentum shallowly concave and moderately emarginate apicomediaally. Maxillary palpi (Figs. 12, 13) 4 segmented, moderately short; ultimate segment about a third longer than penultimate segment; second (pseudobasal) segment with concavity toward the front; ultimate segment articulated toward mouth. Labial palpus, 3 segmented (Figs. 6, 7). Elytron without sutural stria. Prosternum short in front of procoxae (Fig. 3). Tarsal formula, 5-5-5 (Fig. 8). Protarsal claws broad and toothed at base (Figs. 8, 9). Basal segment of metatarsus shorter than second segment. Metatibia without fringe of long natatory setae. First abdominal sternum with longitudinal carina on midline; first and second sterna deeply concave, as in *Chaetarthria* and evident in some *Laccobius*, and sparsely punctate; sterna 3 to 5 densely punctate and pubescent; last sternum rounded apically, without apicomediaal emargination.

Type species of the genus.—*Guyanobius adocetus*, new species.

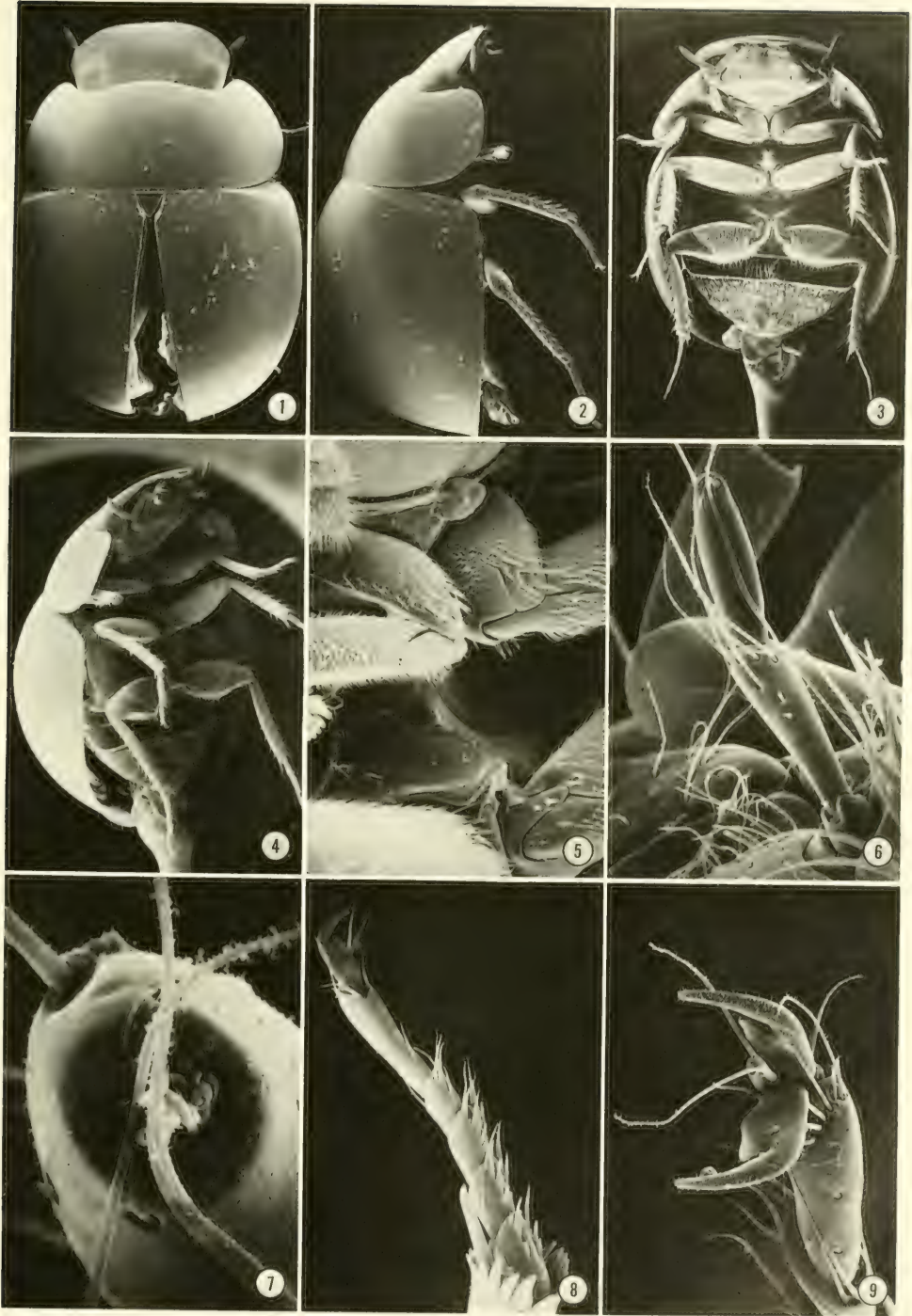
Etymology.—*Guyanobius*, from Guyana, the country in northeastern South America where the type specimen of this genus was collected, plus *bius* from *bios*, G. = life, because this genus forms a part of the fascinating biological diversity of that region. Gender: masculine.

Adults of the genus *Guyanobius* may be distinguished readily from those of other genera assigned to the Hydrobiinae by the presence of the following combination of character states. (1) Prosternum with distinct keel-like process on apicomediaal margin projecting beyond anterior margin of prosternum (Fig. 5) and another keel-like process (visible when disarticulated) on posteromediaal margin which rests in the notched apex of the mesosternum (Fig. 3). (2) Mesosternum with large, broad, triangular protuberance on basal half (Fig. 5). (3) First and second abdominal sterna excavated (Fig. 3) and often filled with a hyaline mass. (4) First abdominal sternum with longitudinal cariniform ridge on midline (Fig. 3). (5) Elytra without sutural stria. (6) Labrum hidden under expanded clypeus.

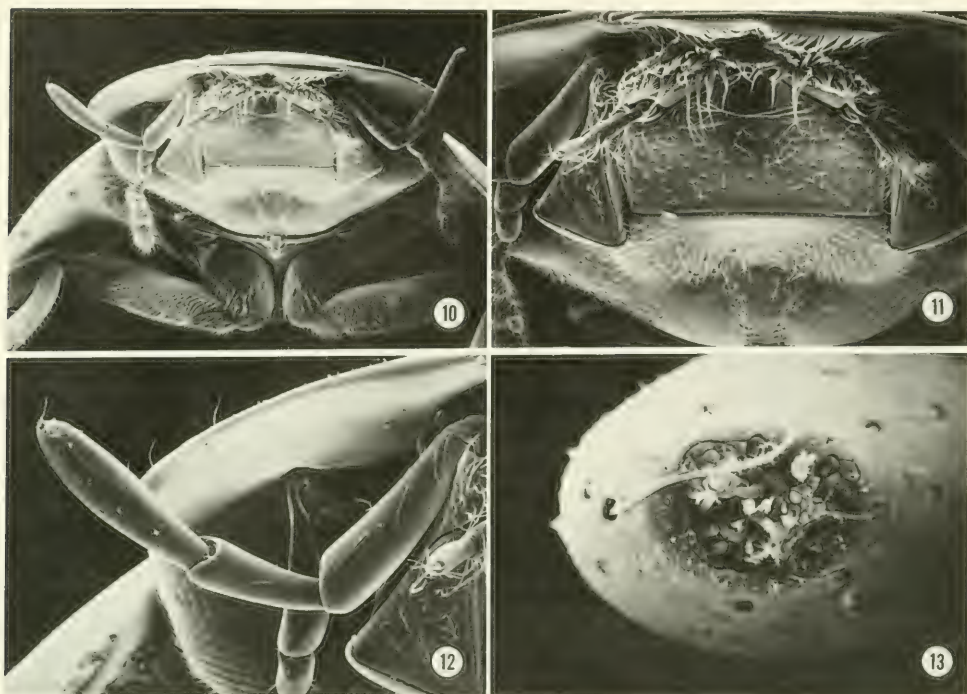
Guyanobius adocetus Spangler, NEW SPECIES

Figs. 1–24

Holotype male.—Form and size: Hemispherical, strongly convex dorsally (Figs. 1–4). Length, 3.5 mm; greatest width, 2.5 mm.



Figs. 1-9. *Guyanobius adocetus*, new species. 1, Habitus, dorsal view, 27 $\times$. 2, Habitus, lateral view, 27 $\times$. 3, Habitus, ventral view, 27 $\times$. 4, Habitus, oblique view, 27 $\times$. 5, Prosternal and mesosternal protuberances, 126 $\times$. 6, Labial palpus, 441 $\times$. 7, Sensilla, apex of labial palpus, 2890 $\times$. 8, Protarsus, 219 $\times$. 9, Protarsal claws, 550 $\times$.



Figs. 10-13. *Guyanobius adocetus*, new species. 10, Head and prosternum, 64 $\times$. 11, Mentum and submentum, 123 $\times$. 12, Maxillary palpus, 187 $\times$. 13, Sensilla, on apex of maxillary palpus, 1450 $\times$.

Coloration: Shiny black dorsally except narrow band on anterior margin of head, lateral margins of pronotum, and very narrow marginal bands on elytra dark reddish brown. Venter dark reddish brown except all palpi, maxillae, mentum, antennae, and tarsi slightly lighter reddish brown.

Head: Very finely, sparsely punctate; punctures on disc separated by 4 to 6 times their diameter; punctures across base of head between eyes smaller and sparser than discal punctures and separated by 3 or 4 times their diameter. Clypeus (Figs. 1-4, 10-12) strongly, broadly expanded anteriorly and laterally, concealing labrum (Figs. 10, 11); lateral margin extending deeply into eye (Fig. 2) and narrowly separated from posterolateral margin of eye; anterior margin feebly arcuate apicomediaally. Mentum shallowly concave, moderately broad, and moderately emarginate apicomediaally; surface moderately coarsely, sparsely punctate; punctures separated by 3 to 5 times their diameter. Submentum shallowly concave and densely, finely punctate; each puncture bearing a seta (Fig. 11).

Thorax: Pronotum widest at posterior third; strongly rounded laterally; shallowly emarginate and feebly arcuate apicomediaally (Fig. 1); truncate posteriorly; narrowly margined laterally and anterolaterally behind eyes; not margined posteriorly except posterolateral angles; sides nearly vertical, extending well below prosternum (Fig. 4); punctures on disc finer than and slightly more widely separated than discal punctures of head; most punctures separated by about 6 to 8 times their diameter; lateral punctures slightly coarser. Prosternum with distinct, keel-like, medial process on anterior third extending beyond anterior margin of

prosternum (Fig. 5) and another on posteromedial margin. Prosternal process very narrow, elongate. Mesosternum with moderately broad, triangular protuberance on posterior half between and slightly in front of mesocoxae (Fig. 5). Metasternum broadly triangularly raised medially; glabrous (except a few setae behind mesocoxae), shiny; sides shallowly concave; metepisterna pubescent. Procoxae sparsely finely setose laterally but with 6 very stout, darker setae ventroapically (Fig. 3). Profemora densely punctate and pubescent on basal two-thirds; mesofemora and metafemora, except apical fourth, densely punctate and pubescent (Fig. 3). Elytra with sides nearly vertical, extending well below mesosternum, metasternum, and abdominal sterna (Fig. 4); without sutural striae; very finely, sparsely punctate; punctures larger than those on pronotal disc and disarrayed except as follows. Each elytron with 2 rows of very coarse punctures and 1 lateral row of moderately coarse punctures extending from humeral area to apical fourth; punctures separated by 1 or 2 times their diameter; widely separated, seta-bearing punctures in 4 additional poorly defined rows, rows indicated by long setae which arise from punctures. Lateral margin of each elytron narrowly rimmed but rim disappearing at about apical fourth. Scutellum flat, triangular; surface finely, sparsely punctate; punctures separated by 3 to 5 times their diameter.

Abdomen: First and second sterna strongly concave and bearing a lens-shaped hyaline mass in concavities as in *Laccobius* and *Chaetarthria*; with coarse, sparse, seta-bearing punctures; punctures separated by 2 to 4 times their diameter. Remaining sterna finely and densely punctate and densely pubescent.

Male genitalia: As illustrated (Figs. 14, 15).

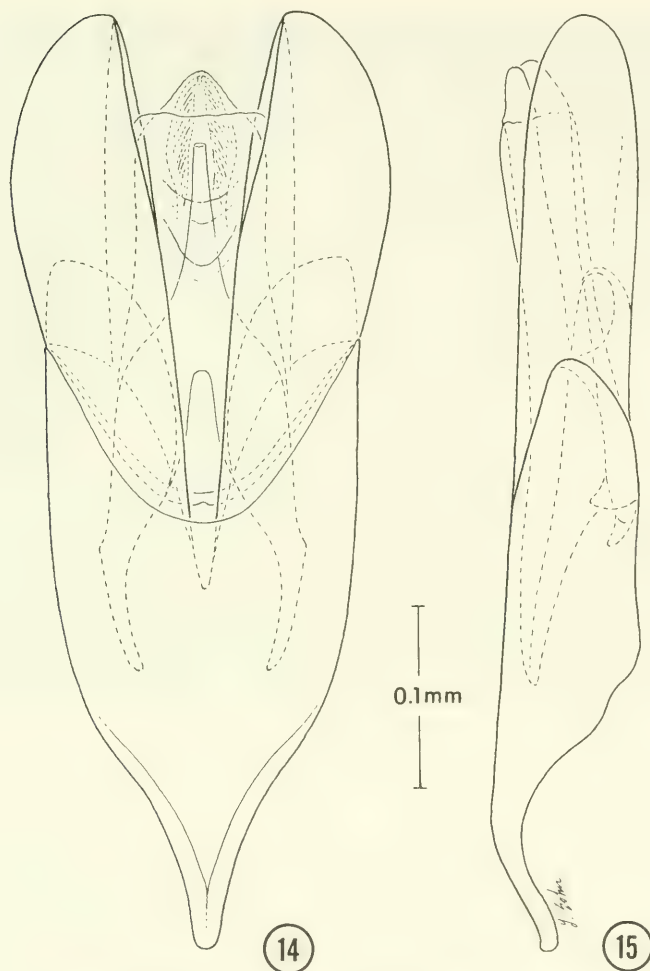
Female.—Similar to male except average size is larger.

Variations.—Males varied in length from 3.1 to 3.4 mm; females varied in length from 3.1 to 3.6 mm.

Type data.—Holotype ♂: GUYANA: MAZARUNI-POTARO DISTRICT: Takutu Mountains, 6°15'N, 59°5'W, 3–10 Dec. 1983, P. J. Spangler, R. A. Faitoute, P. D. Perkins; collected from leaf packs among rocks in shaded stream; deposited in the National Museum of Natural History, Smithsonian Institution. Allotype: Same data as holotype. Paratypes: Same data as holotype, 7 ♂, 8 ♀; same data as holotype except, 3–10 Dec. 1983, 11 ♂, 13 ♀; same data as holotype except, 18 Dec. 1983, P. J. Spangler, W. E. Steiner, and M. Levine, 30 ♂, 20 ♀. SURINAME: BROKOPONDO DISTRICT: Brownsberg Natuurpark, Witi Kreek, 200 m, 25 Aug. 1982, W. E. Steiner, 1 ♀. Paratypes will be deposited in the British Museum (Natural History), London; California Academy of Sciences, San Francisco; Canadian National Collection, Ottawa; Instituto de Zoología Agrícola, Facultad de Agronomía, Maracay, Venezuela; Institut Royal de Historie Naturelle de Belgique, Bruxelles; Museum National de Histoire Naturelle, Paris; Museo Argentina de Ciencias Naturales, Buenos Aires, and the Zoologische Sammlung Bayerischen Staates, München.

Etymology.—Named *adocetus*, from *adoketos*, G. = unexpected, because finding a hydrobiine beetle in a stream in the Takutu Mountain rainforest was a surprise.

Larva of Guyanobius adocetus (Figs. 16–24).—Body elongate (Fig. 16). Total length, 5.02 mm; width of prothorax, 0.89 mm. Color of integument light creamy yellow. Sclerotized head capsule, thoracic and abdominal sclerites, spiracles, legs, abdominal tubercles, and spiracular atrium testaceous. Integument covered dor-



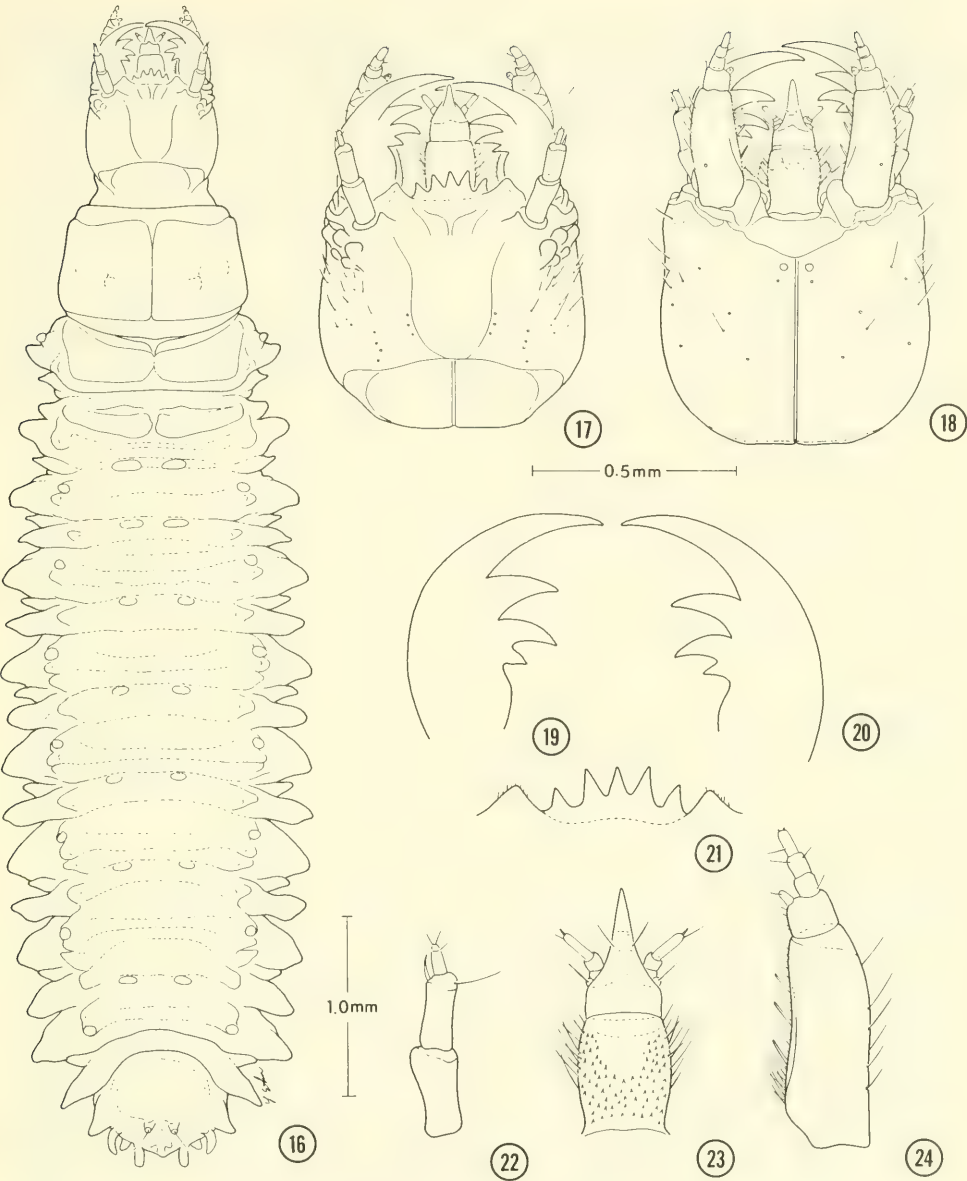
Figs. 14, 15. *Guyanobius adocetus*, new species; male genitalia. 14, Ventral view. 15, Lateral view.

sally with fine, whitish, branchiallike setae intermixed with irregularly spaced short dark asperities.

Head (Figs. 17, 18) quadrangular; 0.66 mm wide, 0.46 mm from labroclypeus to occipital foramen. Frontoclypeal suture feebly indicated. Frontal sutures united at base of head, therefore, without epicranial suture. Frons campanuliform. Cervical sclerites narrow, transverse, and triangular. Ventral surface of head glabrous except 8 setae anterolaterally below each ocellus and behind base of mandible; with 2 deep, posterior tentorial pits medially, a short distance behind gula.

Labroclypeus (Fig. 21) prominent, symmetrical. With 5 large, medial teeth; each lateral tooth slightly shorter than and separated more widely from other three. Middle tooth of labroclypeus slightly narrower than other teeth; each tooth separated from next tooth by a stout yellow seta. Anterolateral projections of epistoma as long as lateral teeth; both projections rounded anteriorly and each bearing numerous large, stout yellow setae apically.

Ocular area each with 6 distinct ocelli arranged in an ellipse; anterior 3 ocelli slightly larger than posterior 3.



Figs. 16–24. *Guyanobius adocetus*, new species, larva. 16, Habitus, dorsal view. 17, Head capsule, dorsal view. 18, Head capsule, ventral view. 19, Left mandible. 20, Right mandible. 21, Labroclypeus. 22, Antenna. 23, Labium. 24, Maxilla.

Antenna (Fig. 22) moderately short, cylindrical, extending almost to base of first segment of maxillary palpus. First and second segments subequal and each about twice as long as last segment; second segment with small apicolateral tubercle and 2 long slender apicomедial setae. Last segment slender, parallel sided, bearing 2 slender distal setae and a minute apicolateral appendage.

Mandible (Figs. 19, 20) symmetrical, prominent, stout, sharply pointed apically; inner surface of each mandible with 2 large, well-defined, medial teeth and 1 small, basal tooth; molar area rounded.

Maxilla (Fig. 24) with stipes stout, elongate, tapering distally; stipes bearing a row of 3 or 4 stout setae on inner margin, and 6 long, slender, yellow setae laterally. Palpifer segmentlike; with slender sclerotized appendage on apicomedial angle; appendage a third as long as palpifer and bearing 1 long apical seta. Palpus 4 segmented; tapering distally; first segment longest, twice as long as palpifer; second and third segment subequal, each slightly more than half as long as basal segment; second segment with 1 long, slender, lateral seta near base; last segment conical, slightly longer than third segment and bearing 1 long seta medially at midlength.

Labium (Fig. 23), including ligula, slightly longer than length of stipes. Ligula elongate, exceeding length of labial palpus. Labial palpus 3 segmented; first segment short and broad; last segment about as long as mentum, bearing a long basal seta at each lateral corner dorsally. Mentum quadrangular; glabrous dorsally; ventrally glabrous except apicolateral corners each with 1 long seta. Submentum slightly wider than mentum; dorsal surface spinose; with numerous, long, stout setae laterally; ventral surface glabrous except long apicolateral setae.

Gula short; transversely pentagonal; shallowly rounded posteromedially (Fig. 18). Two tentorial pits a short distance behind gula.

Prothorax with sides moderately arcuate; posterolateral angles broadly rounded, with a few short setae; anterolateral angles each with a few long setae and a few short setae; sagittal line present. Prosternal sclerite large, subrectangular; sagittal line present.

Mesothorax wider than prothorax and about two-thirds as long (measured on midline); with 2 large, rectangular mesotergal sclerites; laterally, each margin with an elongated spiracular tubercle between 2 setiferous lobes; sagittal line present.

Metathorax slightly wider than and as long as mesothorax; anterior metatergal sclerites short, transverse, subrectangular, larger than posterior sclerites; posterior sclerites small and narrow; sagittal line present.

Legs, 4 segmented. Procoxae large, separated by about length of a trochanter. Trochanter about as long as femur (viewed ventrally). Femur about as long as tibiotarsus. Tarsal claw single, with 2 stout robust setae ventrally at basal third.

Abdomen of 8 distinct segments; ninth and tenth segments reduced. First abdominal segment with 2 small, ovate sclerites; segments 2 to 7 also with similar sclerites but each becoming increasingly smaller. Terga similar to each other. True segmentation obscured by additional transverse folds on segments; segmented folds continued onto sternum. Each segment with 2 folds; numerous asperities scattered randomly over folds. A large spiracular tubercle present on first fold at base of epipleural lobe on abdominal segments 1 to 7. Epipleurites and hypopleurites prominently lobed. Eighth tergum represented by superior valve of stigmatic atrium (Fig. 16) beneath which lies the eighth pair of abdominal spiracles. Ninth tergum trilobed; middle lobe large, with several short, stout setae; lateral lobes smaller, about two-thirds as wide as median lobe, each bearing several short setae on caudal margin.

Larval specimens examined (11): The larvae, along with adults, were berlesed from leaf packs during a period of several days. They are deposited in the U.S. National Museum of Natural History, Smithsonian Institution and are labeled: GUYANA: MAZARUNI-POTARO DISTRICT: Takutu Mountains, 6°15'N, 59°5'W, 3–10 Dec. 1983, P. J. Spangler, R. A. Faitoute, and P. D. Perkins. The

larva of the genus described above keys to the hydrobiine genus *Limnoxenus*, couplet 30, in Bertrand's (1972) generic key to hydrophilid larvae. The genus *Limnoxenus* is treated by some authors (Balfour-Browne, 1958) as a synonym of *Hydrobius* and by others (Lohse, 1971) as a valid genus. D'Orchymont (1919) and Bertrand (1972) also question the validity of the genus. However, whether the genus *Limnoxenus* is valid or not is the subject for another study. For the present purpose the following couplet will separate the larva of *Guyanobius* from the larva of "*Limnoxenus*."

- Length of ligula exceeding length of labial palpus. Length of full grown larva 4 or 5 mm. Guyana and Suriname *Guyanobius* Spangler
- Length of ligula about half as long as labial palpus. Length of full grown larva 12 to 16 mm. Middle Europe, Hawaii, Australia, New Zealand *Limnoxenus* Rey

HABITAT

Adults and larvae of this genus were found living in leaf packs lodged against rocks and logs in and along the banks of a small, shallow, whitewater stream in a densely shaded rainforest. The stream was about 1 to 2 m wide, sloped from the bank to 30 cm in depth, and the substrate was sand, gravel, and rocks. Colorimetric water chemistry tests provided the following data: Oxygen, 9.0 ppm; pH, 5.5; and hardness, 5.0. The water temperature was 24.5°C when most of the specimens were collected.

Some specimens were aspirated from the leaf packs spread apart on a nylon ground cloth; other specimens were obtained by placing leaf packs in cloth berlese funnels for 24–48 hours.

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NOTE

The Altitudinal Range of *Pogonomyrmex pima* (Formicidae: Hymenoptera)

In his book on the harvester ants of the genus *Pogonomyrmex*, Cole (1968, *Pogonomyrmex Harvester Ants. A Study of the Genus in North America*, Univ. Tenn. Press, Knoxville, 222 pp.) summarized the known range of *P. pima* Wheeler as southern Arizona in U.S.A. and Sonora in Mexico. Within that range nests have been found from sea level to elevations of 2400 feet. Following Creighton's view (1956, *Psyche* 63: 54–56) Cole proposed to ignore two localities cited for *pima* by Olsen (1934, *Bull. Mus. Comp. Zool.* 77: 493–514). One disputed record is Bowie, Arizona at 3700 feet. While curating miscellaneous undetermined *Myrmica* specimens in the Museum of Comparative Zoology, Harvard University, I found an unidentified *Pogonomyrmex* worker labeled from Bowie. Comparison with Cole's descriptions and series of identified *pima* and its closest relative *P. imberbiculus* Wheeler, showed without doubt that the specimen belongs to *pima*. Olsen's record is therefore confirmed and the altitudinal range of *pima* confirmed to some 4000 feet.

The other questioned record cited by Olsen (1934, *ibid.*), Mt. Lemmon, South Catalina Mts., Arizona, 8000–9000 feet, appears somewhat out of line, though not impossible. The specimen(s) involved could perhaps be found also in some part of the fragmented W. M. Wheeler Collection of ants.

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A LIST OF THE SPIDERS OF PEPPERMINT IN WESTERN AND CENTRAL OREGON

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Abstract.—Forty-five species of spiders, comprising 36 genera and 13 families, were collected by sweep net and pitfall trap from six peppermint fields in western and central Oregon from May through August 1981. Although the fauna from western Oregon exhibited a higher species richness than that of central Oregon (40 vs. 28 species respectively), the rank order of numerically dominant species was very similar in each region: in western Oregon, the rank order of abundance was *Tetragnatha laboriosa*, *Erigone dentosa*, *Misumenops celer* and *Enoplognatha ovata*; in central Oregon, the most common species collected was *Erigone dentosa*, followed by *Misumenops celer*, *Pardosa sternalis*, and *T. laboriosa*. Thus, the difference in species richness between the two regions is primarily due to the addition of rarer species in western Oregon.

Generalist arthropod predators are potentially important regulators of insect pest populations in Oregon peppermint (Berry, 1977). Although the suite of predaceous insect species found in peppermint is similar to that of other agroecosystems (Hollingsworth, 1981), little is known about the spider fauna. This study was conducted to provide a list of the spider fauna for the two major peppermint growing areas of Oregon.

Peppermint is grown primarily in the Willamette Valley in the western part of the state and on the fringes of the Great Basin Desert in central Oregon. These two areas differ markedly in climate and native vegetation. The Willamette Valley is classified as maritime, having warm, wet winters, warm, dry summers and an average annual precipitation of 120 cm. Forest groves and savannahs dominated by Garry Oak are a conspicuous feature of the Willamette Valley Province (Franklin and Dyrness, 1973). The principle peppermint growing area in central Oregon is in the Columbia Basin Province, characterized by warm, dry summers, cold, dry winters and an average annual precipitation of 40 cm. Bunchgrass and sagebrush dominate this region, with forest vegetation confined to mountain slopes.

Peppermint is harvested in both regions from mid to late August. Because most of the above-ground biomass is removed for oil or for tea production, all foliage dwelling and some ground dwelling arthropod species must annually recolonize the crop from surrounding areas. For this reason, the arthropod fauna that eventually colonizes peppermint over the growing season may have a species composition that is unique to the region within which peppermint grows. Because western and central Oregon differ so markedly in climate and vegetation, any species list for peppermint must incorporate this regional influence.

Table 1. List of spider species collected by sweep net (S) and pitfall trap (P) in central and western Oregon peppermint, May through August 1981. Index of relative abundance: A = abundant, 10% of total individuals collected over the entire sampling period; C = common, between 1% and 10%; R = rare, less than 1%.

Guild and Species	Collecting Method		Relative Abundance	
	S	P	West OR	Cent OR
Orb-Weavers				
<i>Araneus</i> sp. (imm)	X		R	
<i>Araniella displicata</i> (Hentz)	X		R	R
<i>Argiope trifasciata</i> (Forsk.)	X		R	
<i>Metapeira foxi</i> Gertsch & Ivie	X		R	R
<i>Neoscona</i> sp. (imm)	X		C	
<i>Tetragnatha laboriosa</i> Hentz	X		A	C
Space-Web Weavers				
<i>Dictyna oregona</i> Gertsch	X		C	
<i>Dictyna tridentata</i> Bishop & Ruderman	X		C	
<i>Tricholathys rothi</i> Chamb. & Gertsch	X	X	C	
<i>Tricholathys spiralis</i> Chamb. & Ivie		X	R	R
<i>Enoplognatha marmorata</i> (Hentz)	X	X	R	R
<i>Enoplognatha ovata</i> (Clerck)	X	X	C	R
<i>Enoplognatha thoracica</i> (Hahn)	X	X	R	R
<i>Neottiura bimaculatum</i> (L.)	X		R	
<i>Theridion neomexicanum</i> Banks	X			R
Sheet-Web Weavers				
<i>Erigone dentosa</i> O. P. Cambridge	X	X	A	A
<i>Walckenaeria spiralis</i> (Emerton)		X		R
<i>Bathypantes brevipes</i> (Emerton)	X	X	C	R
<i>Lepthyphantes tenuis</i> (Blackwall)	X	X	C	R
<i>Linyphantes</i> sp. (imm)		X	R	
<i>Microlinyphia mandibulata</i> (Emerton)	X		R	
<i>Pimosa altiocularata</i> (Keyserling)	X		R	
<i>Tennesseellum</i> sp.		X	R	
Funnel-Web Weavers				
<i>Agelenopsis</i> sp. (imm)	X		R	
Hunters				
<i>Pardosa dorsuncata</i> Lowrie & Dondale		X	C	C
<i>Pardosa sternalis</i> (Thorell)		X	C	A
<i>Schizocosa mccooki</i> (Montgomery)		X	R	C
<i>Oxyopes salticus</i> Hentz	X	X	R	R
<i>Oxyopes scalaris</i> Hentz	X	X	R	C
<i>Drassyllus depressus</i> (Emerton)		X	R	C
<i>Zelotes fratris</i> Chamberlin		X	R	R
<i>Sergiolus montanus</i> Emerton	X		R	
<i>Micaria</i> sp.		X		C
<i>Misumena vatia</i> (Clerck)	X		C	
<i>Misumenops celer</i> (Hentz)	X	X	A	C
<i>Xysticus cunctator</i> Thorell	X	X		C
<i>Xysticus</i> sp. (imm)	X			C
<i>Apollophanes margareta</i> Lowrie & Gertsch		X	R	R
<i>Tibellus oblongus</i> (Walckenaer)	X		C	
<i>Philodromus</i> sp. (imm)	X		C	R
<i>Thanatus</i> sp. (imm)	X		R	
<i>Eris</i> sp. (imm)	X		C	R
<i>Metaphidippus</i> sp.	X		R	
<i>Phidippus clarus</i> Keyserling	X		R	R
<i>Phidippus</i> sp. (imm)	X		R	R
Total species	34	22	40	28

STUDY SITES AND METHODS

Spiders were collected from a total of six sites in western and central Oregon. In western Oregon, the principle study site (I) was a three year old, 17 hectare field located three km southwest of Monroe (Linn County). Sites II (3 year, 20 ha) and III (2 year, 20 ha) were located at peppermint fields in the central Willamette Valley, approximately 10 km northwest of Albany (Benton County). In central Oregon, a principal site (IV) was a three year old, 25 ha field seven km northeast of Madras, while another major site (V) was a five year old, seven ha field seven km east of Madras. Site VI was a one year old, 15 ha field located 12 km west of Madras. All three central Oregon sites were in Jefferson County.

Beginning in early May 1981, ground spiders were collected at each of the principal sites (I, IV, V) with the use of 12 cm diameter pitfall traps spaced three meters apart in a 4×4 array. Traps were emptied weekly at site I and biweekly at sites IV and V until the peppermint was harvested in late August. Foliage spiders were collected by taking 400, 180° arc sweeps weekly at site I and biweekly at sites IV and V. Sweeps were also taken at irregular intervals throughout the summer at sites II, III, and VI.

RESULTS AND DISCUSSION

A total of 45 species, representing 36 genera and 13 families, were collected from all six sites in the four month study period—40 species from western Oregon and 28 species from central Oregon (Table 1). Although the western Oregon fauna was 40% richer in species, the numerically dominant species were similar in both collections. The four most commonly collected species at site I (western Oregon) were, in rank order, *T. laboriosa*, *E. dentosa*, *M. celer*, and *E. ovata*, while the combined rank order of abundance at sites IV and V (central Oregon) was *E. dentosa*, *M. celer*, *P. sternalis*, and *T. laboriosa*. These five species are all widely distributed: *T. laboriosa* occurs from Lake Chapala, Mexico to southern Alaska (Levi, 1981), and has been recorded in several lists of agricultural species (Yeargan and Dondale, 1974; Culin and Yeargan, 1983; McIver, 1984); *E. dentosa* is a common species in other agricultural fields (Yeargan and Dondale, 1974; McIver, 1984) and species of *Erigone* are known for their excellent aeronautic dispersal ability (Duffy, 1956); *E. ovata* is a common introduced species of the Pacific Northwest and is characteristic of disturbed habitats (Levi, 1957; Moldenke et al., 1986); *M. celer* is our most common Pacific Coast *Misumenops* (Moldenke et al., 1986) and has been collected in shrubs and from both coniferous and deciduous foliage; and *P. sternalis* is a common streamside denizen, widely distributed in Great Basin country (Vogel, 1970; McIver, pers. obs.). So despite the difference in surrounding habitat between peppermint fields planted in western and central Oregon, 23 spider species are shared, including all four species that represent greater than 10% abundance of either fauna. These observations indicate that in an annually disrupted agricultural field such as peppermint, the spider fauna that develops in a single season will reflect, in part, the dominance of common, ubiquitous species that are good dispersers and are tolerant of disturbed habitats.

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NOTES ON TETRASTICHINAE TYPES IN THE ZOOLOGICAL
INSTITUTE, LENINGRAD (HYMENOPTERA: EULOPHIDAE)

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Abstract. — Type specimens of Tetrastichinae (Hymenoptera: Eulophidae) in the Zoological Institute, Leningrad (ZIL) were examined. Lectotypes are designated for the following species: *Tetrastichus coccinellae* Kurdjumov, *Aprostocetus eupatorii* Kurdjumov, *T. pospelovi* Kurdjumov, *T. sokolowskii* Kurdjumov, *T. orchestidis* Bukowsky. Holotypes of the following species are in the collection of the ZIL: *Tetrastichus puncticoxae* Kurdjumov, *T. violaceus* Kurdjumov, *T. bibikovae* Dzhankmen. The primary type of *T. talitzkii* Kostjukov is shown to be a lectotype, not a holotype, and *nikolskajae* is chosen as the correct original spelling for *T. nikolskajae* Kostjukov.

This paper treats tetrastichine (Hymenoptera: Eulophidae) type material in the Zoological Institute, Leningrad (ZIL) in an attempt to stabilize several species names, to bring attention to types that may have previously been considered lost or for which the type depository was not given in the original description, and to treat nomenclatural problems that should be treated through publication. Species of N. V. Kurdjumov, V. Bukowsky, and V. V. Kostjukov are discussed.

Kurdjumov worked at the Poltava Experimental Station, Ukraine, and he described 10 species of tetrastichines. After World War II, M. N. Nikol'skaya brought a Schmidt box representing what was left of his collection to the ZIL. Material found in this box is referred to as from Kurdjumov's collection; material in ZIL but not found in this box is referred to as from ZIL, although in some cases it is assumed that Kurdjumov saw this material.

Material was found, and is discussed below, for all Kurdjumov tetrastichine species except *Geniocerus populi* (1913: 250, 251), *Aprostocetus quadriannulatus* (1913: 252, attributed to Förster, in litt.) and *T. mokrzeckii* (1912a: 144-145). The original description of *mokrzeckii* stated that cotypes of that species were in the Museum of the Crimea, Simferopol.

Also in the ZIL are type specimens for *Tetrastichus orchestidis* Bukowsky (discussed below), *T. bibikovae* Dzhankmen, 1971, and all species described by Kostjukov. Two of Kostjukov's species are discussed in order to select a correct original spelling for *T. nikolskajae* and to clarify the lectotype status of the primary type of *T. talitzkii*.

Tetrastichus cirsii (Kurdjumov)

Aprostocetus cirsii Kurdjumov (Förster in litt.), 1913: 252.

Tetrastichus cirsii (Kurdjumov), Domenichini, 1965: 128; 1966: 24.

This species, attributed to Förster in Kurdjumov's key to *Aprostocetus* (1913), was represented in ZIL by a single damaged specimen (sex unknown) from Förster's collection with the Förster labels "Aachen, Rheinland, Förster" and "*Tetrastichus Cirsii* Foerst., A." Although it is very likely that this specimen was examined by Kurdjumov when he was preparing his key, I hesitate to designate it as lectotype since the abdomen and antennae are missing and the head is crushed and partly missing. Perhaps a better specimen will be found in the future.

***Tetrastichus coccinellae* Kurdjumov**

Tetrastichus scaposus Thomson, 1878: 284.

Tetrastichus coccinellae Kurdjumov, 1912b: 239–240. Lectotype ♀ (present designation), USSR, Ukraine, Poltava (ZIL).

Aprostocetus coccinellae (Kurdjumov), Graham, 1961: 40.

Tetrastichus coccinellae Kurdjumov, Domenichini, 1965: 99; 1966: 26.

In the original description Kurdjumov stated that he examined many ♀ and 3 ♂. Earlier in the paper (p. 236) he indicated that there were at least 30 ♀. In his collection were 27 ♀ and 2 ♂, which I have designated and labeled as lectotype ♀, and 26 ♀, 2 ♂ paralectotypes. Graham (1961) and later Domenichini (1965, 1966) and Kostjukov (1978) chose to use the well-known name *coccinellae* rather than *scaposus* Thomson, 1878, which has priority.

***Tetrastichus eupatorii* (Kurdjumov), comb. n.**

Aprostocetus eupatorii Kurdjumov (Förster in litt.), 1913: 252. Lectotype ♀ (present designation), Germany, Aachen (ZIL).

This species, attributed to Förster in Kurdjumov's key to *Aprostocetus*, was represented in the ZIL collection by 2 ♀ from Förster's collection mounted on a single minuten pin and with the Förster labels "Aachen, Rheinland, Förster" and "*Tetrast. Eupatorii* Först." Domenichini (1966: 60) listed this species under species incertae sedis et nomina dubia and considered the type as probably lost. Since other material has not been found for this species, and since these specimens were almost certainly ones examined by Kurdjumov, I am designating and have labeled these as lectotype ♀ (lower specimen on the minuten) and paralectotype ♀ (upper specimen on the minuten). This previously unplaced species belongs in the *crino* species group (Graham, 1961; Domenichini, 1965), and will be treated by M. W. R. de V. Graham in his forthcoming work on European Tetrastichinae.

***Tetrastichus pospelovi* Kurdjumov**

Tetrastichus pospelovi Kurdjumov, 1912b: 237–238. Lectotype ♀ (present designation) (ZIL).

Geniocerus pospelovi (Kurdjumov), Kurdjumov, 1913: 251.

Aprostocetus pospelovi (Kurdjumov), Graham, 1961: 47.

Tetrastichus pospelovi (Kurdjumov), Domenichini, 1965: 120; 1966: 45.

Kurdjumov mentioned a total of 2 ♀ and 2 ♂ with the original description. A female was in his collection with the label "*Tetrastichus pospelovi*," and I have designated and labeled it as lectotype. Other specimens appear to be *pospelovi*; however they were not labeled, and there are more specimens (7 ♀, 1 ♂, and 1 ♀ of a different species on three pins) than mentioned in the original description. I

have not designated these specimens as paralectotypes, but I have labeled them as being from Kurdjumov's collection and placed them under *pospelovi* in the ZIL collection.

***Tetrastichus puncticoxae* Kurdjumov**

Tetrastichus puncticoxae Kurdjumov, 1913: 253, 255. Holotype ♀, USSR, Ukraine, Poltava (ZIL).

Tetrastichus puncticoxe Kurdjumov, Domenichini, 1966: 47.

The unique female mentioned in the original description was in Kurdjumov's collection with the label "*puncticoxae*, sp.n." I have clearly labeled this as being the holotype.

***Tetrastichus sokolowskii* Kurdjumov**

Tetrastichus sokolowskii Kurdjumov, 1912b: 238–239. Lectotype ♀ (present designation) (ZIL).

Tetrastichus sokolowskii Kurdjumov, Kurdjumov, 1913: 254.

Aprostocetus sokolowskii (Kurdjumov), Graham, 1961: 39.

Tetrastichus sokolowskii Kurdjumov, Domenichini, 1965: 116; 1966: 49.

The original description mentions 18 ♀ and 2 ♂. There were 6 ♀ and 1 ♂ in Kurdjumov's collection. I have designated and labeled these as lectotype ♀, and 5 ♀, 1 ♂ paralectotypes.

***Tetrastichus violaceus* Kurdjumov**

Tetrastichus violaceus Kurdjumov, 1913: 253, 254–255. Holotype ♀, USSR, Ukraine, Poltava (ZIL).

The unique female mentioned in the original description was in Kurdjumov's collection with the label "*violaceus*, sp.n." I have clearly labeled this as being the holotype.

***Tetrastichus orchestidis* Bukowsky**

Tetrastichus orchestidis Bukowsky, 1938: 168–169. Lectotype ♀ (present designation) USSR, Crimea (ZIL).

Geniocerus orchestidis (Bukowsky), Erdős, 1954: 359.

Aprostocetus orchestidis (Bukowsky), Graham, 1961: 47.

Tetrastichus orchestidis Bukowsky, Domenichini, 1965: 122; 1966: 42.

In the original description Bukowsky stated that this species was described from many specimens. There were 6 ♀ and 4 ♂ in the ZIL with the Bukowsky label "*Tetrastichus orchestidis* n.sp." I have designated and labeled these as lectotype ♀, and 5 ♀, 4 ♂ paralectotypes.

***Tetrastichus talitzkii* Kostjukov**

Tetrastichus talitzkii Kostjukov, 1978: 451. Lectotype ♀, USSR, Moldavia.

Tetrastichus talitzkii was originally described by Kostjukov in his key to *Tetrastichus* in the Handbook of Insects of the European Part of the USSR (1978). It was not treated as a new species in the key because a separate paper describing this species had been submitted for publication several years earlier and was

supposed to be published before the key. This paper was never published. For this reason the original description in the key was not accompanied by a holotype designation or by any reference to type material; the specimens he based his description on thus automatically becoming syntypes.

In an attempt to rectify this situation Kostjukov redescribed *T. talitzkii* (1984a), but with the redescription designated a holotype and paratypes instead of lectotype and paralectotypes. According to article 74a of the International Code of Zoological Nomenclature (1985), this "holotype" is the lectotype, the "paratypes" are paralectotypes. Proper data for all types are as follows.

Lectotype ♀: USSR, Moldavia, Starye Dubossary, from tortricid larva on apple, 10.vii.1974 (Talitzky).

Paralectotypes: as lectotype, 13 ♀, 3 ♂ on 2 cards, 1 ♀, 1 ♂, ♀ antennae (from card mounted paralectotype) on 3 slides; as lectotype but 10–14.vii.1974, 5 ♀, 3 ♂ on 1 card; as lectotype but 30.vi.1974, 10 ♀ on 1 card.

All types in ZIL. Lectotype is on a card with 7 ♀, 2 ♂ paralectotypes and is indicated with red ink.

Tetrastichus nikolskajae Kostjukov

Tetrastichus nikolskajae Kostjukov, 1984b: 30–31.

In the paper containing the original description for this species, the name *nikolskajae* is spelled in two different ways. Through a printer's error the name was spelled as *nikolskaie* where it accompanied the original description (p. 30); however it was spelled *nikolskajae* in two other places in the paper (p. 34, 35), in the English summary to the paper (p. 35), and all the type material (in ZIL) is labelled as *nikolskajae*. Even though the spelling *nikolskaie* was due to a printer's error, there is nothing found in the original publication to indicate which spelling was preferred by the author, and the correct spelling must be chosen by the first reviser. Acting in this capacity, I am selecting *Tetrastichus nikolskajae* as the correct spelling; the spelling *nikolskaie* is an incorrect original spelling and has no standing in nomenclature.

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NOTE

Baetis magnus, new species, formal new
name for *Baetis* sp. B of Morihara and McCafferty
(Ephemeroptera: Baetidae)

Morihara and McCafferty (1979. Trans. Am. Entomol. Soc. 105: 139–221) described two unique larval specimens from Arizona and New Mexico as *Baetis* sp. B. Although an adequately comparative description was presented, a formal name and new species were not established because of the paucity of material and knowledge of species variability at that time. Since then, we have examined over 200 similar specimens from western U.S.A., especially the Pine Ridge area of far western Nebraska, that fully substantiate the existence of a distinctive yet unnamed species as was earlier hypothesized.

Therefore, with reference to the description of *Baetis* sp. B (pp. 161–162) and figure 20 (p. 195) of Morihara and McCafferty (1979), we hereby establish the name *Baetis magnus* NEW SPECIES to replace the previous informal name *Baetis* sp. B Morihara and McCafferty. We furthermore designate the types of *B. magnus* as follows: Holotype: larva, Nebraska, Dawes Co., Squaw Cr, V-30-1984, R. Lawson & K. Brown, Purdue Univ. Entomol. Res Coll. (PERC). Paratypes: 3 larvae, same data and deposition as holotype; 1 larva, Arizona, Yavapai Co., Verde R, IV-9-1968, R. Koss & R. Baumann (slide mounted in balsam, solvent xylene), PERC; 10 larvae, NE, Dawes Co., Chadron St Prk, Chadron Cr, VI-25-1984, R. Lawson, PERC; 3 larvae, NE, Sioux Co., Sowbelly Canyon Cr, V-28-1984, R. Lawson & K. Brown, PERC; 38 larvae, NE, Dawes Co., Rapid Cr below Pactola Dam, VII-22-1977, R. Lawson & K. Brown, U.S. Ntl. Museum; 38 larvae, NE, Dawes Co., West Ash Cr, V-25-1984, R. Lawson & K. Brown, California Acad. Sci.; 1 larva, New Mexico, Grant Co., Cherry Cr, 14 mi N Silver City, IX-9-1967, R. Koss (slide mounted, balsam), PERC.

Mature larvae of *B. magnus*, which range in length from 7 to 13 mm (not including caudal filaments), resemble large larvae of *Baetis tricaudatus* Dodds, a species also placed in the *rhodani* group (Morihara and McCafferty, 1979). Even in the field, however, these two species are separable by the more elongate gills of *B. magnus* (length ca. $1.5 \times$ width) vs. those of *B. tricaudatus* (length subequal to width). Whereas *B. tricaudatus* is a widespread, variable, and relatively ubiquitous species in North America, *B. magnus* apparently is found only disjunctly in small, mostly spring-fed streams of the West, sometimes coexisting with *B. tricaudatus*. Additional characteristics that distinguish *B. magnus* were given by Morihara and McCafferty (1979), but note that *B. magnus* will key to *B. sp. A*, not *B. sp. B*, in the larval key presented there due to an inadvertent transcription error. Because we possess only one reared female subimago of *B. magnus* and one associated but not reared male adult, and because adults of the *rhodani* group are essentially inseparable at the species level on the basis of current information, any description of the adult at this time would be tenuous.

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NOTE

The Correct Type Species of *Peridiplosis* (Diptera: Cecidomyiidae)

When Felt (1918. N.Y. State Mus. Bull. 202: 160) described *Peridiplosis*, he designated *Cecidomyia quercina* Felt as type and sole species. In the synonymy that immediately preceded the redescription of *quercina*, Felt (ibid.: 160) listed references to two separate species named *quercina*, effectively synonymizing the two there for the first time. The earlier available name is *Cecidomyia quercina* Felt (1907a. N.Y. State Educ. Dept., Albany: 41 [a preprint of Felt, 1907b. N.Y. State Mus. Bull. 110: 137]). This species is represented by one type specimen: it was collected in New York and bears Felt's unique note number, 342. The later available name is *Dicrodiplosis* (correctly *Dicrodiplosis*) *quercina* Felt (1907c. N.Y. State Educ. Dept., Albany: 19 [a preprint of Felt, 1908. N.Y. State Mus. Bull. 124: 300]), also represented by one specimen, this one collected in Georgia and labeled with the unique Felt number, 1006. Both types are in the Felt Collection, which is presently on loan from the New York State Museum in Albany to the Systematic Entomology Laboratory, Washington, D.C. The two species are distinct and not synonyms: *Cecidomyia quercina* belongs in *Trisopsis* (Gagné, 1973. Ann. Entomol. Soc. Am. 66: 881) and *Dicrodiplosis quercina* in *Dicrodiplosis* (Gagné, ibid.: 869). On the basis of Felt's designation, *Peridiplosis* would be a synonym of *Trisopsis* Kieffer (1912). However, Felt's (1918, ibid.) description of *Peridiplosis* and redescription of *quercina* clearly described *Dicrodiplosis quercina*. In addition, the type locality was given as Georgia (not also New York), the male antenna of *Dicrodiplosis quercina* was illustrated, and Felt cited the type no. 1006. Felt's designation of *Cecidomyia quercina* is obviously a misidentified type species according to Article 70b of the International Code of Zoological Nomenclature (1985, 3rd edition, International Trust for Zoological Nomenclature). Cases involving a misidentified type species are supposed to be referred for adjudication to the International Commission on Zoological Nomenclature, but a proposal to amend Article 70b has recently been made (Sabrosky, 1984. Bull. Zool. Nomen. 41: 156-158). The relevant part of that proposed amendment to the present case is as follows: "if . . . a misidentification has clearly occurred, [a person] . . . is to continue to regard as type species the species that was actually involved, but under its correct name, and not the species represented by the name incorrectly applied to the type species." I have not written to the Commission about this case pending a decision by the Commission on Sabrosky's proposal, but I regard *Peridiplosis* Felt (1918) as clearly a synonym of *Dicrodiplosis* Kieffer (1895). In Gagné (ibid.) I recognized *Peridiplosis* as a synonym of *Dicrodiplosis* but did not realize then the problem of the misidentified type species.

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BOOK REVIEW

The Leafhoppers and Planthoppers. Edited by L. R. Nault and J. G. Rodriguez. John Wiley & Sons, New York. 1985. 500 pp. \$59.95.

For many years, I have harbored a secret wish—to write a book about my favorite taxon, the leafhoppers (Homoptera: Cicadellidae). After all, I have actively explored the morphology, pathology, physiology, ecology, evolution, taxonomy and (of course) the ability of these insects to transmit viruses and mollicutes. Now, within the last decade, books on this subject, all collections of chapters, have begun to emerge. The latest and the best is *The Leafhoppers and Planthoppers*, edited by L. R. Nault and J. G. Rodriguez (John Wiley & Sons, New York, 1985).

The addition of the planthoppers (Homoptera: Fulgoroidea), which was necessitated by their roles in transmitting important plant diseases—e.g. coconut lethal yellowing—made even more difficult the task of producing an integrated text, with parallel treatment of each of the major taxa. The leafhoppers and planthoppers have, after all, been separated since at least the Triassic, 200 million years ago. Thus, there has been an abundance of time for divergence of form, function, and physiology of the two groups. In a sense such “natural experiments” on a grand evolutionary time scale have much to offer us in our quest for an understanding of nature, since commonalities in strategy, particularly if derived by convergent evolution, must, after 200 million years, be driven in large part by ecological forces.

Few of the authors of the 19 chapters of this book attempted comparison of the two groups. Exceptions were chapters by E.-D. Ammar on internal morphology and ultrastructure, and Elaine Backus on anatomical and sensory mechanisms of feeding behavior. Ammar's chapter featured original electron micrographs and like the Backus chapter, was illustrated as copiously as publisher's constraints would permit. Both of these chapters managed to be both comparative and detailed.

Systematics and external morphology of the groups were covered in chapters by M. W. Nielson (cicadellid taxonomy), H. D. Blocker and B. W. Triplehorn (cicadellid morphology), and L. B. O'Brien and S. W. Wilson, who covered both aspects for the planthoppers.

A concise and focussed chapter on acoustic behavior of leafhoppers and planthoppers by M. F. Claridge dealt, of necessity, largely with leafhoppers, but discussed the implications of sonic communication, via substrate, in relation to speciation. The recent work of this author and his colleagues, using rice insects as models, is one of the most exciting recent new areas of leafhopper biology. The implications of leafhoppers and planthoppers for rice culture are discussed by M. R. Wilson and Claridge in a separate chapter.

In a few cases, the task assigned for individual chapters was too large. Marion Brooks struggled valiantly with “Nutrition, Cell Culture and Symbiosis of Leafhoppers and Planthoppers,” and A. H. Purcell engaged in a similar struggle with “The Ecology of Bacterial and Mycoplasma Plant Diseases Spread by Leafhoppers

and Planthoppers.” This breadth was especially evident when juxtaposed with a chapter by A. van Schoonhoven on breeding for resistance to *Empoasca* leafhoppers in dry beans. Even with this disparity, however, the bean chapter proves to be entertaining, and one can if desired leaf to the broader review chapter of W. M. Tingey on plant defensive mechanisms.

Ecologists will find the chapters by L. V. Madden on population dynamics, and migratory behavior by R. A. J. Taylor, of special interest. Of special interest also will be the emerging story of maize hoppers and the viruses and mollicutes that they transmit. This story is especially fascinating in that maize agriculture represents, perhaps, the most readily “tracked” case history of land turnover from native vegetation to agriculture. Thus, there is a good opportunity to document the factors involved when insects are converted into pests by human activities. The chapters by L. R. Nault and R. Gamez and P. Leon discuss these issues explicitly.

Chapters on insect parasites of cicadellids (P. H. Freytag), and pathogens of cicadellids and planthoppers (R. S. Soper), although narrowly posed, reflect a general neglect that cannot be blamed on the authors.

Finally, of course, there is the matter of plant disease transmission, which stimulated much of the work in the individual chapters. One will find a chapter by M. Conti on virus transmission, but a chapter on mollicute transmission is absent. This seems a strange omission, since Nault himself has contributed so much towards such a chapter. I suspect that reviews by P. Markham in other publications may have seemed too fresh. Indeed, when one considers the amount of writing that had preceded this volume, one must be impressed by the generally fresh perspective that it offers.

The above warm praise should not be construed as an opinion that this book is perfect. I read most of it rather carefully, and found some troubling errors and omissions. There are too many misspelled binomial names, for example. There are discussions of *r*- and *K* selection without citation of MacArthur and Wilson’s classic works from which the theory emerged. Only Purcell cites the extensive ecological and epidemiological work of Kiritani and his associates, who understood and incorporated, among other things, predator-prey theory into their field research.

These are only a few examples. In general, I noted a distressing tendency of most—or perhaps all—authors to plunge off the deep end as they wandered from their main areas of expertise. This should not be construed as a criticism of any author, or even editor, but of the process of assembling books. It is true that the selection of authors of this book leans heavily toward the Ohio group of L. R. Nault. But in a volume dedicated to D. M. DeLong—who indelibly inscribed Ohio on the leafhopper map—this does not seem inappropriate. It does mean that there is a natural geographical bias in the views of the authors.

The bottom line, however, is that I felt, after reading the book, a little chastened by the knowledge that if I had written any of these chapters, I perhaps would also have wandered astray when I left areas in which I was less than familiar. We are living at a time when sufficient details are available from massive amounts of research to bury almost any overview that a generalist might develop. Certainly, the dream of having, between two covers, a synopsis of information about a very

interesting group of insects has been realized. But perhaps the leafhoppers—and certainly the planthoppers as well, in their own right—are natural books so large that no single digest can be assembled that will ever give them full justice.

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PROC. ENTOMOL. SOC. WASH.
88(3), 1986, p. 608

BOOK NOTICE

Entomology of the California Channel Islands: Proceedings of the First Symposium. A. S. Menke and D. R. Miller, editors. Santa Barbara Museum of Natural History, Santa Barbara, CA 93105. 178 pp, paper (from a symposium held in 1981 at the Entomological Society of America meeting in San Diego).

Practically all the contributors use the term preliminary to describe the state of knowledge of the insect fauna of the California Channel Islands. In fact, only Orthoptera have been adequately surveyed on all the islands. Yet this volume is useful for summarizing the considerable data that does exist for various groups of insects, and should stimulate renewed efforts to investigate the relationships of the fauna. Contributions range from a detailed biogeographic analysis of Orthoptera to updated checklists (e.g. Coleoptera of Santa Barbara Island). All are largely based on recent collecting by specialists so that the number of species known from most islands has swollen enormously since the early lists of Cockerell (e.g. over 450 species of Lepidoptera from Santa Cruz). Inclusion of taxa as ecologically diverse as mealybugs, bees, sphecids wasps and Lepidoptera allows some initial comparison of different distributional patterns and their likely causes. One new subspecies, *Bembix americana dugi* Menke, is described. The book is prefaced by a historical summary and ended by a supplement to the earlier bibliography by Miller and Menke. It is accompanied by an excellent set of topographic maps.

This will be a valuable work for those interested in island biology, for all systematists dealing with taxa which occur on the California Channel Islands, and should also be called to the attention of those with a bent for the natural history of the insects of southern California.

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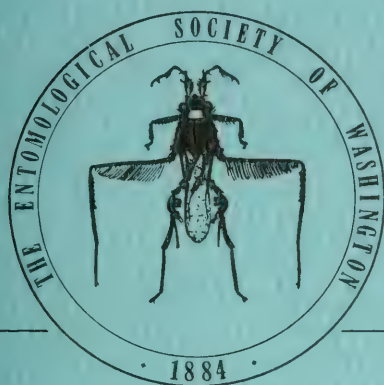
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Please see p. 730 of the July 1984 issue for information regarding preparation of manuscripts.

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**DERMACENTOR TICKS (ACARI: IXODOIDEA: IXODIDAE) OF THE
NEW WORLD: A SCANNING ELECTRON MICROSCOPE ATLAS**

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Abstract.—The cosmopolitan, mostly Holarctic genus *Dermacentor* is represented in the New World by 12 species, some of which are important vectors of disease to man and animals. Existing diagnostic keys, usually based on line drawings, are useful principally to specialists or to those with access to reference specimens. We have investigated New World *Dermacentor* spp. by scanning electron microscopy (SEM) and found salient characters useful in identification by the nonspecialist. A key to females and males of New World species, illustrated by SEM photographs, is presented. Listings of geographical distribution and disease relationships are given for each species.

From a combined medical and veterinary standpoint, the most important ticks of North America are species of the genus *Dermacentor*. Existing diagnostic keys to taxa within this genus are based on national confines or subdivisions (Cooley, 1938; Gregson, 1956; Brinton et al., 1965; Strickland et al., 1976; Furman and Loomis, 1984). However, the predilection of many *Dermacentor* spp. for livestock or other large mammals that range widely or are regularly transported by man compromises the reliability of these keys. In addition, key characters are conventionally illustrated by pen and ink drawings, a device adequate for taxonomic specialists but of limited utility to field workers and those without access to reference specimens. Recently, the scanning electron microscope (SEM) has been employed to illustrate morphological features in descriptive and comparative studies of ticks (Keirans et al., 1982; Clifford et al., 1983; Hoogstraal et al., 1983) and has proven particularly useful in diagnostic keys (Keirans and Clifford, 1978; Sonenshine, 1979). We have identified and illustrated salient characters of New

World *Dermacentor* spp. by use of scanning electron microscopy and present keys to males and females. The keys were designed so that they may be used by investigators lacking access to an SEM or to voucher specimens; it is believed that they will facilitate preliminary identification of field-collected specimens by entomologists, parasitologists, epidemiologists, public health workers, veterinarians and other nonspecialists.

No attempt has been made to produce complete descriptions of species. Adequate written descriptions may be found in the existing literature (see below), which should be consulted in order to confirm tentative diagnoses made by use of these keys. We also provide updated information on geographic distribution, based largely on unpublished records of the Rocky Mountain Laboratories (RML) tick collection, now permanently housed in the Entomology Department, Museum Support Center, Smithsonian Institution, Washington, D.C.

This work is dedicated to Dr. Harry Hoogstraal (1917–1986), our colleague and our friend.

DISTRIBUTION

Ticks of the genus *Dermacentor* are members of the acarine family Ixodidae and, together with those of the genera *Cosmiomma*, *Anomalohimalaya*, *Rhipicentor*, *Rhipicephalus*, *Boophilus* and *Margaropus*, form the subfamily Rhipicephalinae. The genus *Dermacentor* is cosmopolitan in distribution and may be encountered on all continents except Australia; however, the species have apparently evolved in the Nearctic Region, where the greatest biological diversity is displayed (Belozеров, 1976). In the New World, 12 species comprise about 40% of the world's total (Table 1). Here, the geographic range of the genus extends from Canada to Argentina, with the largest number of species being located in North America including Mexico. The latter are: *D. (Anocentor) nitens* Neumann 1897, *D. (Dermacentor) albipictus* (Packard 1869) (= *Ixodes nigrolineatus* Packard 1869), *D. (D.) andersoni* Stiles 1908 (= *D. venustus* Marx in Neumann 1897), *D. (D.) halli* McIntosh 1931, *D. (D.) hunteri* Bishopp 1912, *D. (D.) occidentalis* Marx 1892, *D. (D.) parumapertus* Neumann 1901, and *D. (D.) variabilis* (Say 1821). Of these, only three species, *D. (D.) albipictus*, *D. (D.) andersoni*, and *D. (D.) variabilis*, are found north of the U.S.-Canada border, while some are also found in Central or South America. The tropical horse tick, *D. (A.) nitens*, ranges from the southern United States throughout most of the American tropics to northern Argentina; *D. (D.) albipictus* has been reported in Guatemala, and *D. (D.) halli*, as far south as Panama. Two *Dermacentor* species are restricted to Central America: *D. (D.) dispar* Cooley 1937, and *D. (D.) latus* Cooley 1937; a third species, *D. (D.) dissimilis* Cooley 1947, is found in Mexico and Central America. A fourth Neotropical species, *D. (D.) imitans* Warburton 1933, occurs in both Central America and northwestern South America.

MEDICAL AND VETERINARY IMPORTANCE

Ticks are the most important vectors to domestic animals of agents of infectious disease and are second only to mosquitoes as transmitters of pathogenic microorganisms to man. In addition, ticks, including dermacentors, may cause a deadly paralysis in man and animals through injection of a toxin, as well as death of

Table 1. New World *Dermacentor* ticks: distribution and hosts.

Tick	Distribution	Hosts
<i>D. nitens</i>	Tropical and subtropical areas of North, Central and South America, including Caribbean and Galapagos Is.	All stages: equids and ruminants
<i>D. dispar</i>	Central America	Adults: peccary, deer
<i>D. dissimilis</i>	Mexico, Central America	All stages: equids and ruminants
<i>D. parumapertus</i>	W USA; Mexico	All stages: principally lagomorphs, but deer and cattle are also attacked
<i>D. imitans</i>	Mexico; Central and South America	Adults: principally tapirs, but also other larger mammals, including man Immatures: small mammals
<i>D. halli</i>	Texas, USA; Mexico; Central America	Adults: larger mammals, including man Immatures: small mammals
<i>D. latus</i>	Central America	Adults: principally tapirs
<i>D. hunteri</i>	SW USA; Sonora and Baja California Norte, Mexico	Adults: principally desert bighorn sheep
<i>D. albipictus</i>	Canada, USA, Mexico, Central America	All stages: principally ruminants and equids, rarely on man
<i>D. occidentalis</i>	Pacific Coast of North America from Oregon, USA to NW Mexico	Adults: larger mammals, including man Immatures: small mammals
<i>D. andersoni</i>	Western Canada and USA	Adults: larger mammals, including man Immatures: small mammals
<i>D. variabilis</i>	Central and E Canada; USA east of Rocky Mountains; E Mexico to Yucatan; also localized foci of California, Oregon, Washington and Idaho, USA	Adults: medium and large-sized mammals, including man Immatures: small mammals

heavily parasitized animals through exsanguination. Other effects of tick-feeding on livestock and wildlife include anemia, weakness, weight loss, tick worry, secondary infection or invasion of tick-bites by microorganisms or screwworms, damage to hides and udders, and loss of drayage capability and manure (Furman and Loomis, 1984; Strickland et al., 1976; Anonymous, 1984). Old World dermacentors, particularly in Europe and Asia, are involved in the transmission to domestic animals of *Anaplasma ovis*, *Babesia bovis*, *B. caballi*, *B. canis*, *B. equi* and *Theileria ovis*. They are also important vectors of Congo-Crimean hemorrhagic fever, Russian spring-summer encephalitis, *Rickettsia siberica*, Q-fever and tularemia, which cause human disease. A list of agents and disease conditions transmitted or caused by the various species of New World dermacentors is given in Table 2.

Table 2. New World *Dermacentor* ticks: involvement in human and animal disease.*

Agent	Disease	Host	Vectors
<i>Rickettsia rickettsi</i>	Rocky Mountain spotted fever	Man, various wild mammals	<i>D. andersoni</i> , <i>D. variabilis</i> , <i>D. occidentalis</i> <i>D. albipictus</i> (?)
<i>Rickettsia rickettsi</i>	Rocky Mountain spotted fever	Lagomorphs	<i>D. parumapertus</i>
<i>Coxiella burnetii</i>	Q-fever	Man, livestock	<i>D. andersoni</i> , <i>D. variabilis</i> , <i>D. occidentalis</i>
<i>Chlamydia</i> sp.	Psittacosis	Man, various wild mammals	<i>D. andersoni</i> (?), <i>D. occidentalis</i> (?)
<i>Anaplasma marginale</i>	Anaplasmosis	Cattle	<i>D. andersoni</i> , <i>D. variabilis</i> (?), <i>D. occidentalis</i> , <i>D. albipictus</i> (?)
<i>Francisella tularensis</i>	Tularemia	Man, various wild mammals	<i>D. andersoni</i> , <i>D. variabilis</i> , <i>D. occidentalis</i>
<i>Francisella tularensis</i>	Tularemia	Lagomorphs	<i>D. parumapertus</i>
<i>Babesia caballi</i>	Piroplasmosis	Horses	<i>D. nitens</i>
<i>Orbivirus</i>	Colorado tick fever	Man, various wild mammals	<i>D. andersoni</i> , <i>D. variabilis</i> (?), <i>D. albipictus</i> (?), <i>D. occidentalis</i> (?), <i>D. parumapertus</i> (?)
<i>Flavivirus</i>	Powassan encephalitis	Man, various wild mammals	<i>D. andersoni</i>
Toxin	Tick paralysis	Man, dogs, ruminants, equids	<i>D. andersoni</i> , <i>D. variabilis</i> , <i>D. occidentalis</i>

* Skin wounds predisposing to infection or screwworm attack, anemia, weakness, weight loss and death may occur in wild and domestic ruminants and equids infested with *D. nitens* or *D. albipictus*.

MATERIAL EXAMINED

Specimens used for scanning electron microscopy were prepared by the method of Corwin et al. (1979). Specimens examined for this study are summarized in Table 3.

GLOSSARY OF TERMS FOR USE WITH THE KEYS

- Basis capituli: The basal portion of the capitulum of a tick on which the mouthparts are attached (Figs. 1, 16a).
- Cervical grooves: A pair of grooves in the scutum extending posteriorly from anterior angles or "shoulders" of the scutum; may be shallow or deep, faint or absent (Fig. 10).
- Cornua: Small projections extending from the dorsal, posterolateral angles of the basis capituli (Figs. 51, 52).
- Coxae: Small sclerotized plates on the venter representing the first segment of the legs (Figs. 5-8).
- Dorsal prolongation: The posterodorsal extension of the spiracular plate (Figs. 22-24).
- Emarginate: A section cut out or removed from the margin of the scutum.
- Eyes: Simple light-gathering organs located on the lateral margins of the scutum in both adults and immatures.

Table 3. *Dermacentor* spp. examined by scanning electron microscopy.

RML #	Species	Host	Locality	Date	Collector
23576	<i>D. albipictus</i>	<i>Alces alces</i>	Montana, USA	III.1947	G. Kohls, J. Brennan and W. Jellison
—	<i>D. andersoni</i>	RML Laboratory colony			
47638	<i>D. dispar</i>	<i>Dasypus novemcinctus</i>	Belize	II.1967	C.W.B. Hatherill
28469	<i>D. dissimilis</i>	Horse	Guatemala	XI.1950	H.T. Dalmat
29323	<i>D. halli</i>	Porcupine	Guatemala	IV.1951	H.T. Dalmat
11355	<i>D. hunteri</i>	<i>Ovis canadensis</i>	Arizona, USA	X.1935	G.M. Kohls
37973	<i>D. imitans</i>	<i>Tayassu tajacu</i>	Panama	V.1962	P. Gallindo
48959	<i>D. imitans</i>	<i>Homo sapiens</i>	Colombia	V.1967	G.B. Fairchild
34927	<i>D. latus</i>	Tapir	Panama	XII.1953	R. Hartmann
13302	<i>D. nitens</i>	Unknown	Nicaragua	V.1937	A. Fouseck
58857	<i>D. occidentalis</i>	On flag	Oregon, USA	IV.1972	R.A. Gresbrink
9265	<i>D. parumapertus</i>	<i>Lepus californicus</i>	Nevada, USA	VI.1940	G.M. Kohls and H. Sargent
—	<i>D. variabilis</i>	RML Laboratory colony	Virginia, USA		D. Sonenshine

- Festoons:

Uniform rectangular areas, separated by distinct grooves, located on the posterior body margin in females (Figs. 3, 4) and on the posterior scutal margin in males (Fig. 46).
- Genital grooves:

Long paired grooves diverging from each side of the genital opening and extending to the posterior body margin (Figs. 5, 6).
- Genital opening:

External opening of the genital organs. Located anteriorly on the ventromedian line, posterior to the basis capituli (Figs. 15, 17–18).
- Goblet cells:

Small, round structures located in the spiracular plate (Figs. 19–30). They may be small and numerous as in *Dermacentor variabilis* or large and few as in *D. nitens*.
- Hypostome:

Median ventral holdfast organ of the mouthparts that lies parallel to and between the palps and is immovably attached to the basis capituli. It bears recurved “teeth” or denticles (Figs. 1, 2).
- Hypostomal dentition:

Refers to the arrangement of denticles on the ventral aspect of the hypostome. The number of files of denticles is expressed by the dental formula. Thus, 3/3 dentition means that there are three files of denticles on each side of the median line of the hypostome.
- Lateral grooves:

The grooves running along the sides of the scutum in male *Dermacentor* species (Figs. 32, 34).
- Palps:

Paired articulated appendages located anterolaterally on

the basis capituli (Figs. 1, 2). The sequence of numbering of the segments is by Arabic numerals 1–4, with 1 being the proximal segment (closest to the basis capituli). Segment 4 is usually reduced to a small setae-crowned papilla lying in a cuplike depression of segment 3.

- Spiracular plates: Paired plates located ventrolaterally and posterior to coxa IV; they may be oval, round or comma-shaped (Figs. 19–30). They contain the openings of the respiratory system.
- Trochanter: The second leg segment located distal to the coxa (Fig. 16).

THE GENUS *DERMACENTOR* IN THE NEW WORLD

KEY TO ♀¹

1. Hypostomal dentition 4/4, palpal segment 4 terminal (Fig. 1); festoons 7 (Fig. 3); scutum inornate; spiracular plate with few (e.g. 7) very large goblet cells (Fig. 19); tropical and subtropical areas of North, Central and South America, including Caribbean and Galapagos Is.; on equids and ruminants *D. (Anocentor) nitens*
- Hypostomal dentition generally 3/3 (variable in *D. dissimilis*), palpal segment 4 subterminal and ventral (Fig. 2); festoons 10 or 11 (Fig. 4); scutum usually ornate, spiracular plate with numerous goblet cells of small to moderately large diameters *D. (Dermacentor) spp.* 2
2. Spurs of coxa I widely divergent (Figs. 5, 8) or only a single spur on coxa I (Fig. 7) 3
- Spurs of coxa I with proximal edges apposed or subparallel (Figs. 6, 14) 7
3. With a single spur on coxa I; genital opening surrounded by a circular groove (Fig. 7); goblet cells of spiracular plate homogeneously small and extremely numerous (Fig. 20); Texas, USA, Central America; on peccary and deer *D. dispar*
- With two spurs on coxa I; genital groove truncate anteriorly (Figs. 5, 6, 8, 12); goblet cells of spiracular plate various 4
4. Spiracular plate not comma-shaped (without dorsal prolongation), with relatively few (e.g. 36), moderately large goblet cells (Fig. 21); scutum emarginate at shoulders and posterolaterally (Fig. 9); internal coxal spurs II–IV absent (Fig. 8); hypostomal dentition variable (e.g. 4/4, 4/3, 3/4, 3/3); Central America; principally on horses and cattle *D. dissimilis*
- Spiracular plate comma-shaped (with dorsal prolongation), with many small to large goblet cells (Figs. 22–24); scutum not emarginate (Figs. 10, 11); internal coxal spurs II–IV present or absent; hypostomal dentition 3/3 5
5. Most scutal setae arising from large, deep, evenly distributed pits; cervical grooves as long, deep troughs that widen and become shallower and rugopunctate posteriorly (Fig. 10); ornamentation of scutum, if present,

¹ Size ranges of goblet cells expressed as: small ($\leq 10\ \mu\text{m}$), medium ($10\text{--}20\ \mu\text{m}$), moderately large ($20\text{--}40\ \mu\text{m}$), very large ($> 50\ \mu\text{m}$).

- restricted to a whitish band on posterior margin and/or cervical groove area; central goblet cells of spiracular plate moderately large (Fig. 22); genital opening “V”-shaped (Fig. 12); SW United States and NW Mexico; principally on lagomorphs *D. parumapertus*
- Most scutal setae arising from small shallow punctations; cervical grooves subcircular, short, deep, more pitlike than troughlike (Fig. 11); ornamentation of scutum extensive; goblet cells small to medium; genital opening “U”-shaped, (Figs. 5, 13) 6
6. Goblet cells of spiracular plate all small (Fig. 23); genital opening surrounded by a demarcation; external coxal spurs II–IV short, broad; internals lacking (Fig. 5); Central America; principally on peccary *D. imitans*
- Goblet cells of mixed sizes, small to medium (Fig. 24); genital opening not posteriorly demarcated; coxae II–IV with long, narrow external spurs, II and III with short, broad internals (Fig. 13); SW United States, Central America; on various mammals, including man *D. halli*
7. Genital opening surrounded by circular groove, internal spur of coxa I longer than external (Fig. 14); spiracular plate with numerous homogeneously medium-sized goblet cells and a short, broad dorsal prolongation (Fig. 25); Central America; principally on tapirs *D. latus*
- Without above combination of characters 8
8. Dorsal prolongation of spiracular plate absent or reduced, plate surface nearly filled with moderately large goblet cells, bordered peripherally with, at most, a line of small pores (Fig. 26); internal spurs on coxae II and III; genital opening “U”-shaped (Fig. 6); North and Central America; principally on ruminants and equids *D. albipictus*
- Dorsal prolongation of spiracular plate present, usually well-developed; goblet cells of various sizes and distributions; internal spurs of coxae II and III present or absent; genital opening “U” or “V”-shaped 9
9. Spiracular plate with fewer (e.g. 50 or less) moderately large, widely spaced goblet cells; minute pores, if present, restricted mostly to dorsal prolongation (Fig. 27); genital opening “U”-shaped, containing paired labia (Fig. 15). SW United States, Mexico; principally on desert bighorn sheep *D. hunteri*
- Spiracular plate with numerous (e.g. 90 or more) close-set, small to moderately large goblet cells surrounded by one or more concentric rows of minute pores that extend into dorsal prolongation; genital openings various, but without labia; on medium-sized and large mammals, including man 10
10. Dorsal spur of trochanter I and cornua of basis capituli as long as or longer than wide (Fig. 16a); goblet cells of spiracular plate moderately large (Fig. 28); scutal punctations mostly small, sizes not greatly disparate; genital opening “V”-shaped (Fig. 17); Pacific coast, from Oregon, USA to Mexico *D. occidentalis*
- Dorsal spur of trochanter I and cornua wider than long (Fig. 16b); goblet cells small or moderately large; dorsal punctations of markedly disparate sizes, large and small; genital opening “U”-shaped (Fig. 18) 11
11. Goblet cells of spiracular plate moderately large, few; dorsal prolongation

- of plate narrow (Fig. 29); western areas of Canada, United States
..... *D. andersoni*
- Goblet cells of spiracular plate small, numerous; dorsal prolongation of plate broadly produced (Fig. 30); central and E areas of Canada and United States through E Mexico to Yucatan, also localized in California, Oregon, Washington, and Idaho *D. variabilis*

THE GENUS *DERMACENTOR* IN THE NEW WORLD

KEY TO ♂^{1,2}

1. Hypostomal dentition 4/4, palpal segment 4 terminal (Fig. 1); festoons 7 (Fig. 3); lateral grooves absent (Fig. 31); spiracular plate with few (e.g. 7), very large goblet cells (Fig. 19); spurs of coxae I widely divergent, those of II–IV well developed; tropical and subtropical areas of North, Central and South America, including Caribbean and Galapagos Is.; on equids and ruminants *D. (Anocentor) nitens*
- Hypostomal dentition generally 3/3 (variable in *D. dissimilis*), palpal segment 4 subterminal and ventral (Fig. 2); festoons 11 (Fig. 4); lateral grooves present or absent (Fig. 32); spiracular plate with numerous goblet cells of small to moderately large diameters *D. (Dermacentor) spp.* 2
2. Spurs of coxa I widely divergent (Figs. 5, 8) or only a single spur on coxa I (Fig. 7) 3
- Spurs of coxa I with proximal edges apposed or subparallel (Figs. 6, 14) 9
3. Each coxa with a single spur (Fig. 33); lateral margins of scutum produced as elevated ridges extending from eyes to spiracular plates, these ridges separated from festoons by deep clefts (Fig. 34); goblet cells of spiracular plate homogeneously small and extremely numerous (Fig. 20); Texas, USA, Central America; on peccary and deer *D. dispar*
- One or more coxae with paired spurs; scutum not as above; goblet cells various 4
4. Spiracular plate oval or subcircular (lacking dorsal prolongation) with relatively few (e.g. 33) moderately large goblet cells (Fig. 21); lacking lateral grooves on scutum and internal spurs on coxae II and III; coxae IV not greatly elongated proximally (Fig. 35); hypostomal dentition variable (e.g. 3/3, 3/4, 4/3, 3.5/3.5, 4/4; Central America; principally on horses and cattle *D. dissimilis*
- Spiracular plate with dorsal prolongation (variable in *D. albipictus*), goblet cells various but usually numerous (Figs. 22, 25, 26); lateral grooves of scutum and internal spurs of coxae II and III present or absent; coxae IV much longer proximally than distally (Fig. 36); hypostomal dentition 3/3 5
5. Most scutal setae arising from large deep pits, of which those of lateral groove coalescing, rugopunctate (Fig. 37); ornamentation of scutum usually reduced; spiracular plate comma-shaped, dorsal prolongation rela-

¹ Some features shared by sexes are figured for ♀ only.

² Size ranges of goblet cells as in ♀.

- tively long and narrow (Fig. 22); SW United States and NW Mexico; principally on lagomorphs *D. parumapertus*
- Most scutal setae arising from small pits or shallow depressions, of which those associated with lateral groove discrete (Fig. 38); scutum ornate; dorsal prolongation of spiracular plate often reduced or absent, when present arising from a broad base 6
6. External spur of coxa I longer than internal (Figs. 39, 50) 7
- External spur of coxa I shorter than internal (Fig. 45) 8
7. Goblet cells of spiracular plate all small, dorsal prolongation short, broadly rounded apically (Fig. 41); cornua longer than wide, broadly rounded apically (Fig. 43); spurs of coxae II-IV and most ventral setae reduced (Fig. 39); Central America; principally on tapirs *D. imitans*
- Goblet cells of mixed sizes, small to medium; dorsal prolongation long, apex as wide as base (Fig. 42); cornua wider than long, with blunt points (Fig. 44); coxal spurs and ventral setae normally developed (Fig. 50); SW United States, Central America; on various mammals, including man *D. halli*
8. Lateral grooves absent, but suggested by a linear row of deep pits extending from vicinity of eyes to festoons (Fig. 46); scutal setae shorter than diameter of pits that contain them; spiracular plate with numerous (e.g. >300), close-set, medium sized goblet cells (Fig. 25). Central America; principally on tapirs *D. latus*
- Lateral grooves absent or visible for only a short distance anterior of festoons (Fig. 49); scutal setae longer than containing pits; spiracular plate with fewer than 100 moderately large, goblet cells (Fig. 26). North and Central America; principally on ruminants and equids . . . *D. albipictus*
9. Spiracular plate with long, attenuate dorsal projection and about 50 moderately large, widely spaced goblet cells; minute pores restricted mostly to dorsal prolongation (Fig. 47); SW United States, and Sonora and Baja California Norte, Mexico; principally on desert bighorn sheep . . . *D. hunteri*
- Dorsal prolongation of spiracular plate shorter, less acute; goblet cells numerous (e.g. >90), close set, small to moderately large, and surrounded by one or more concentric rows of minute pores that extend into dorsal prolongation (Fig. 48); on medium-sized and large mammals, including man 10
10. Basis capituli longer than wide; dorsal spur of trochanter I and cornua of basis capituli as long as or longer than wide (Fig. 16a); cornua prominently elevated above median longitudinal area of basis (Fig. 51); sizes of scutal punctations not greatly disparate; pearl gray coloration of scutum more extensive than brown; Pacific coast, from Oregon, USA to Mexico *D. occidentalis*
- Basis capituli and cornua, as well as dorsal spur of trochanter I wider than long (Fig. 16b); cornua not prominently elevated above median longitudinal area of basis (Fig. 52); scutal punctations of markedly disparate sizes, ornamentation varying 11
11. Goblet cells of spiracular plate small, numerous (e.g. >300), dorsal prolongation broadly produced (Fig. 53); Central and E areas of Canada and

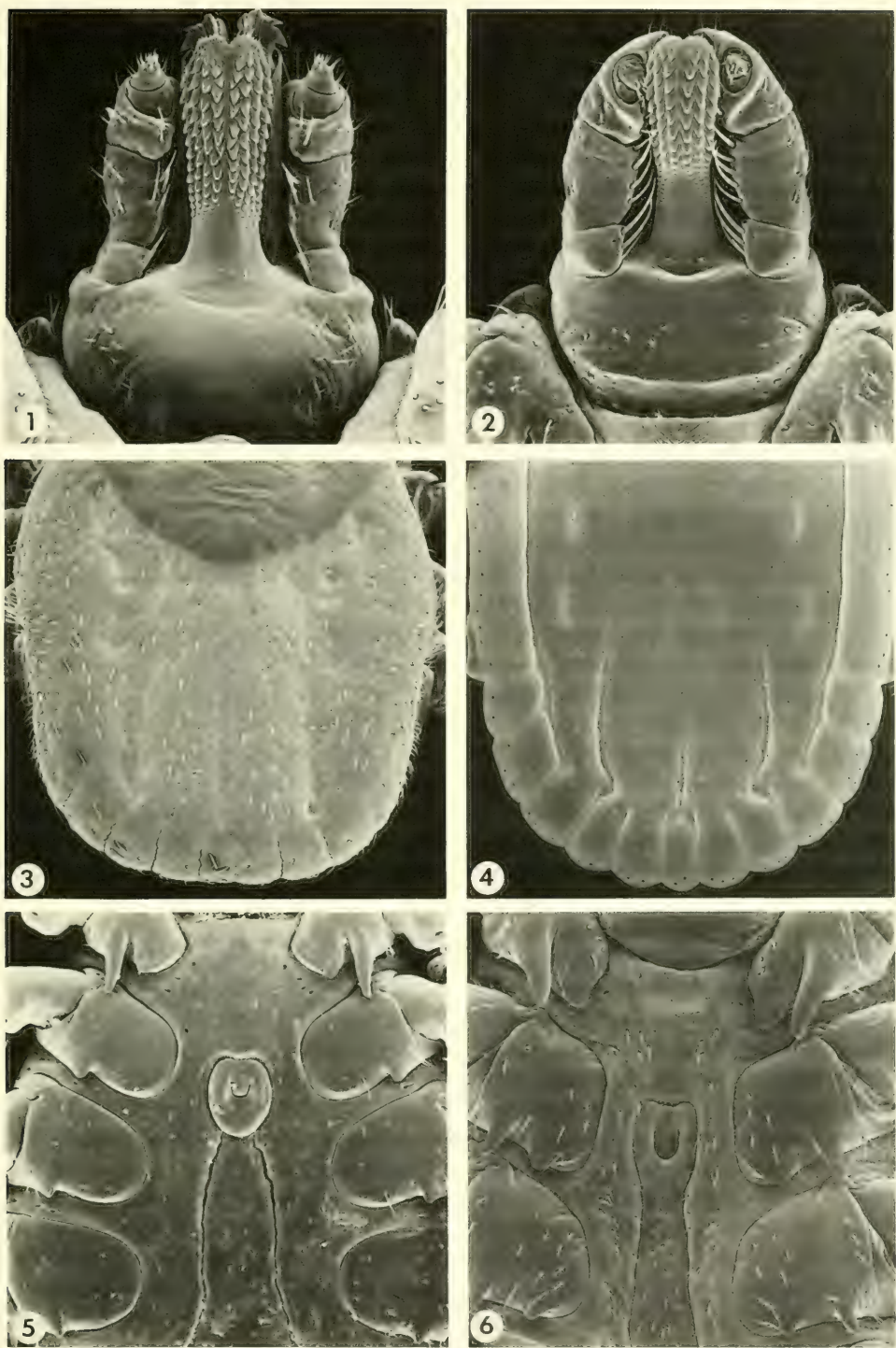
- United States through E Mexico to Yucatan; also in localized foci of California, Oregon, Washington and Idaho *D. variabilis*
- Goblet cells of spiracular plate moderately large, fewer than 100, dorsal prolongation narrower (Fig. 54); western areas of Canada, United States and Mexico *D. andersoni*

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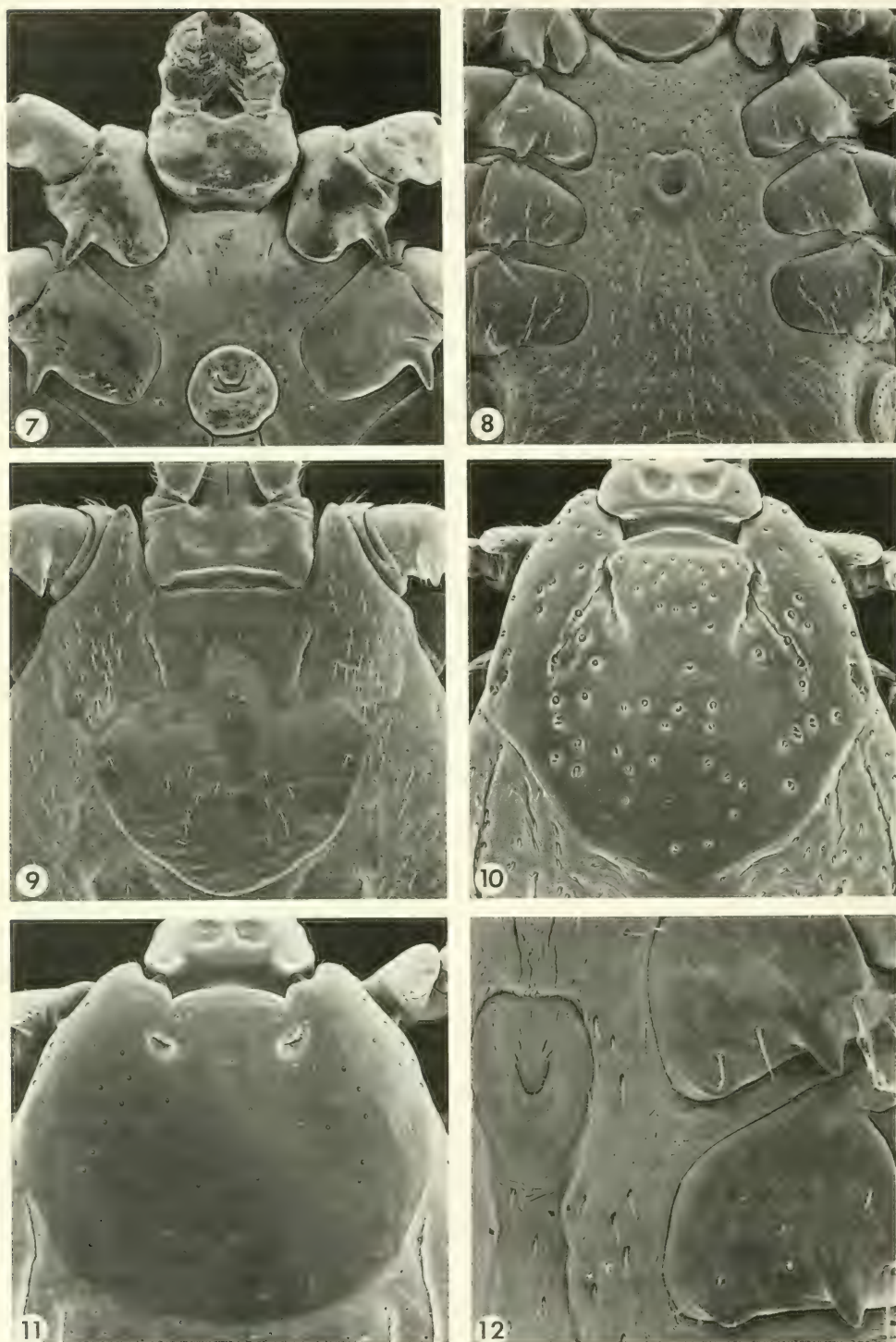
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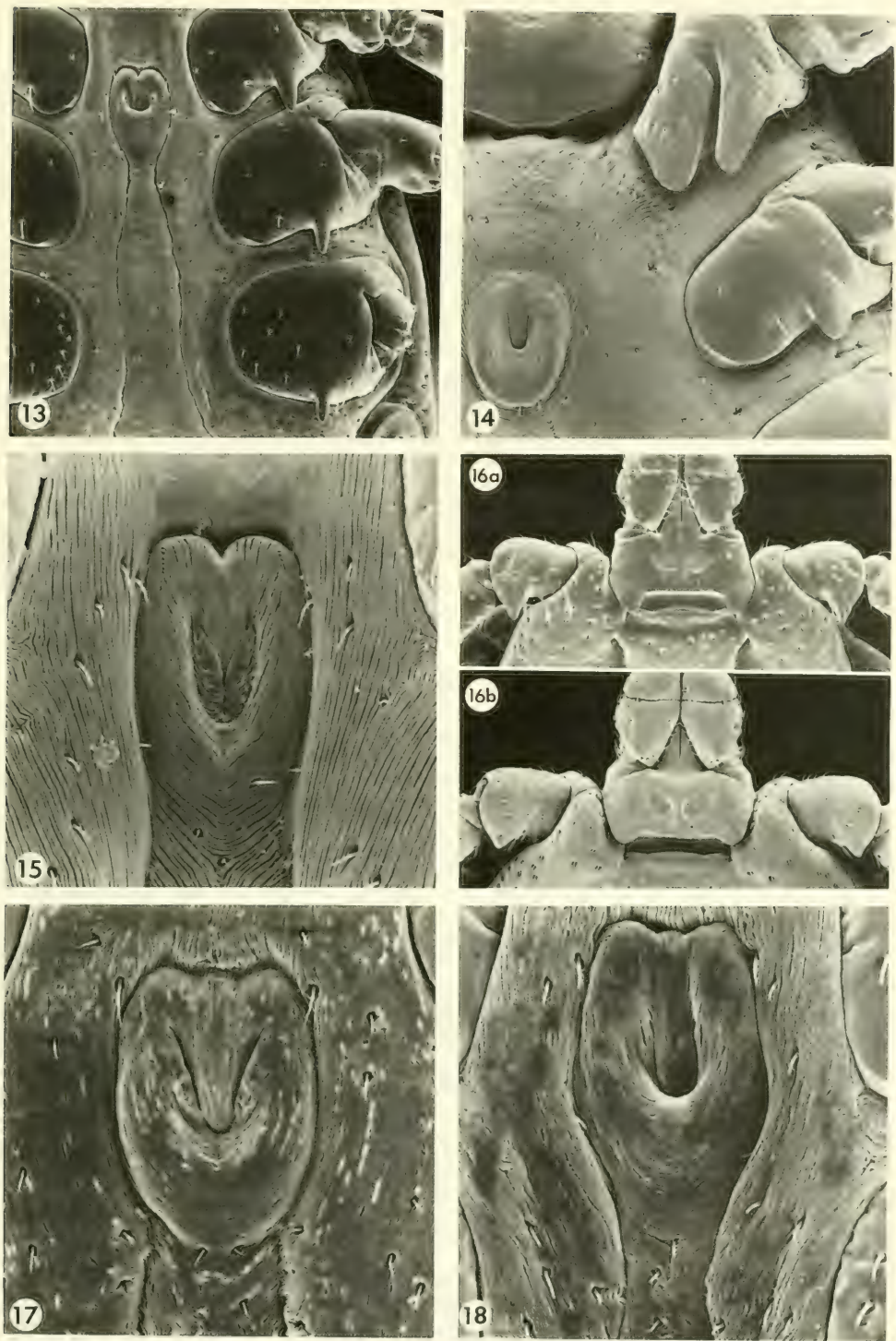
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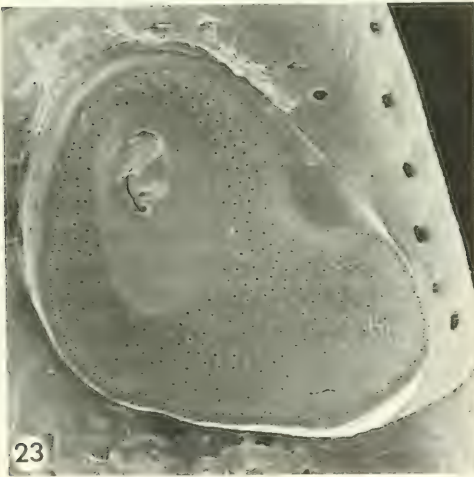
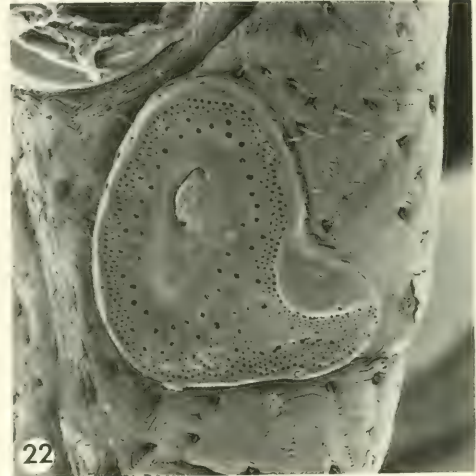
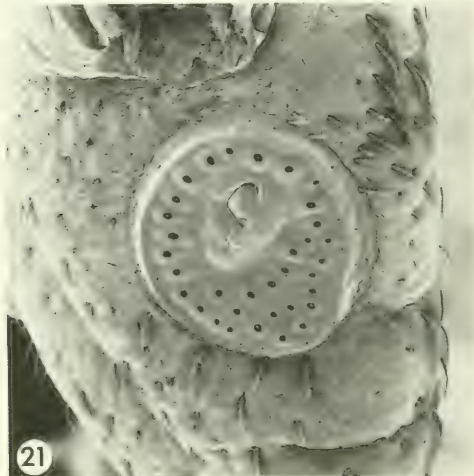
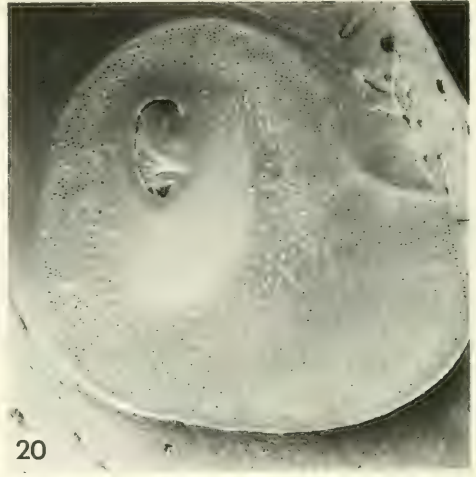
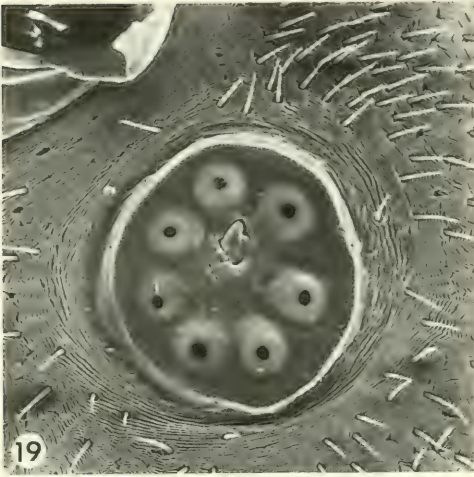
Figs. 1-6. ♀ *Dermacentor* spp. 1, *D. (Anocentor) nitens* capitulum, ventral view, 160×. 2, *D. (D.) imitans*, capitulum, ventral view, 160×. 3, *D. (A.) nitens*, festoons, dorsal view, 70×. 4, *D. (D.) imitans*, festoons, 70×. 5, *D. (D.) imitans*, coxae I-IV and genital opening, 68×. 6, *D. (D.) albipictus*, coxae I-III and genital opening, 77×.



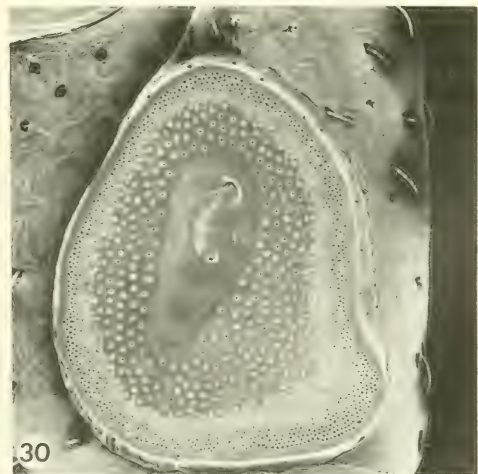
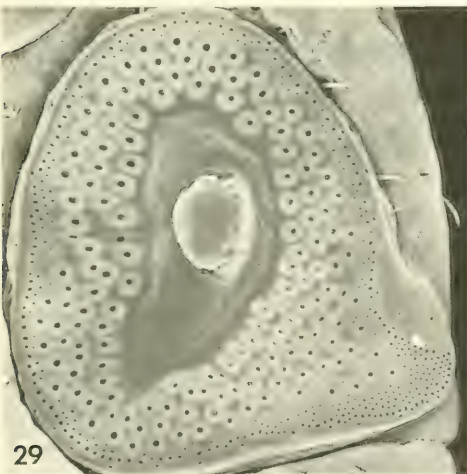
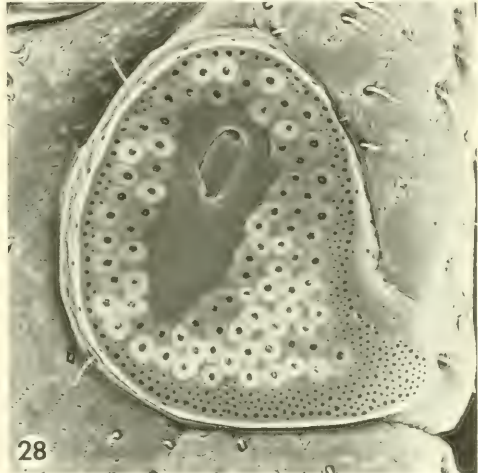
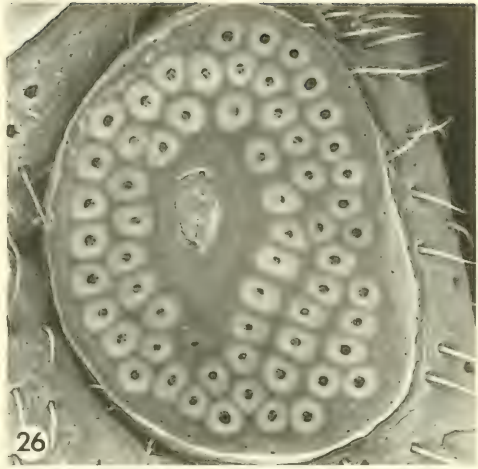
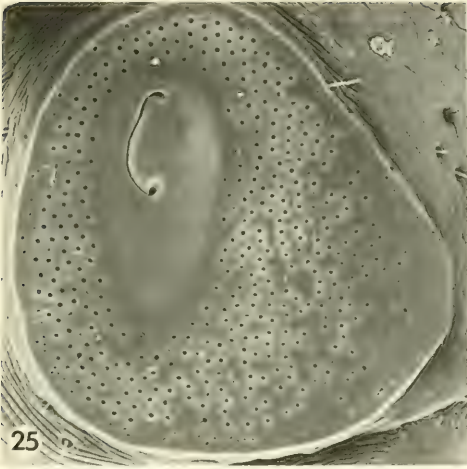
Figs. 7-12. ♀ *Dermacentor* (*Dermacentor*) spp. 7, *D. dispar*, venter of capitulum, coxae I and II and genital opening, 53 $\times$. 8, *D. dissimilis*, coxae I-IV and genital opening, 72 $\times$. 9, *D. dissimilis*, scutum, 90 $\times$. 10, *D. parumapertus*, scutum, 77 $\times$. 11, *D. imitans*, scutum, 67 $\times$. 12, *D. parumapertus*, coxae II and III and genital opening, 188 $\times$.



Figs. 13-18. ♀ *Dermacentor* (*Dermacentor*) spp. 13, *D. halli*, coxae II-IV, genital opening, 76×. 14, *D. latus*, coxae I and II, genital opening, 85×. 15, *D. hunteri*, genital opening, 200×. 16a, *D. occidentalis*, anterodorsal aspect, showing spurs of trochanter I and cornua, 62×. 16b, *D. andersoni*, anterodorsal aspect, showing spurs of trochanter I and cornua, 58×. 17, *D. occidentalis*, genital opening, 220×. 18, *D. andersoni*, genital opening, 240×.



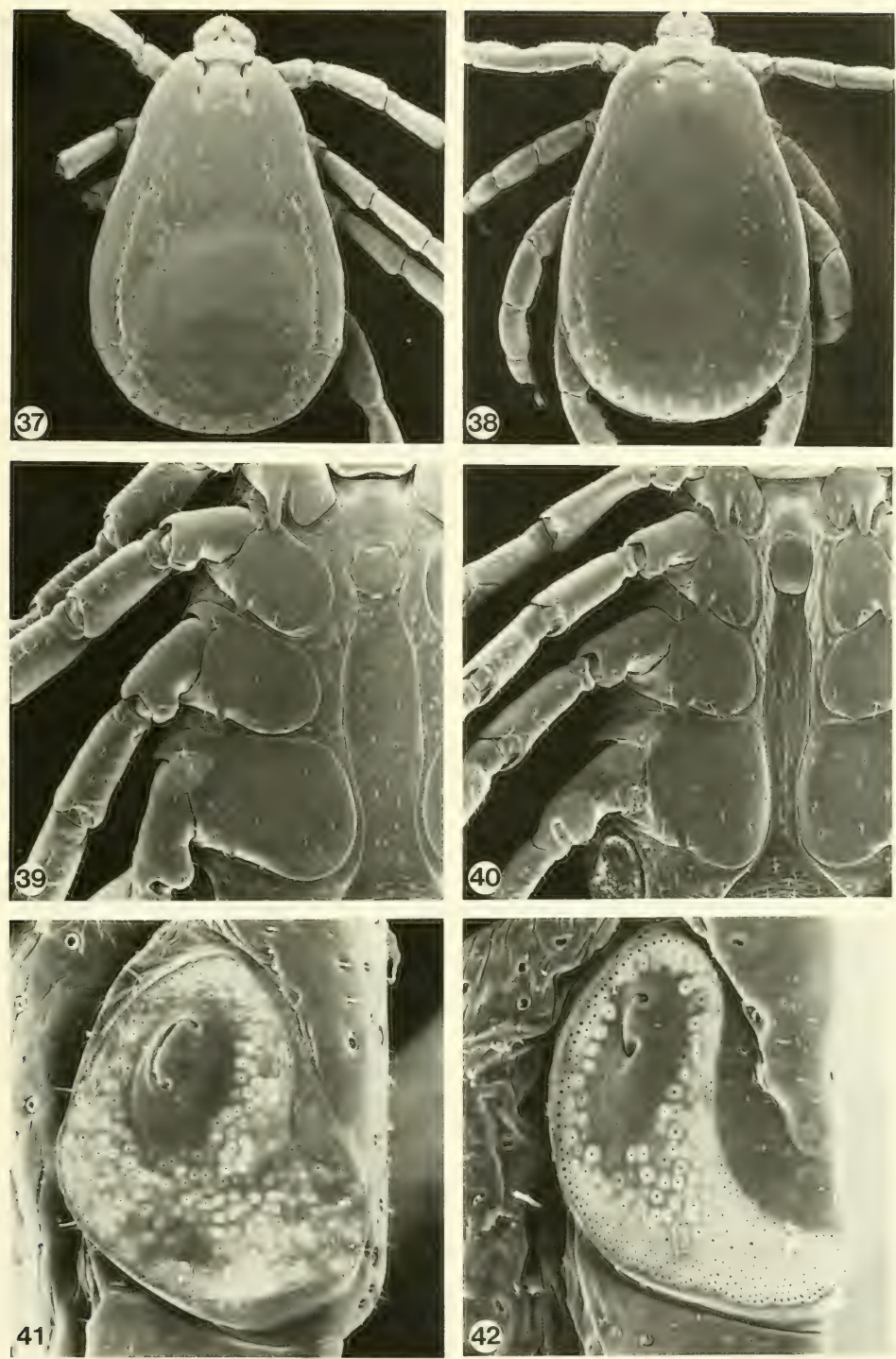
Figs. 19–24. ♀ *Dermacentor* spp., left spiracular plates. 19, *D. (Anocentor) nitens*, 190×. 20, *D. (D.) dispar*, 180×. 21, *D. (D.) dissimilis*, 200×. 22, *D. (D.) parumapertus*, 200×. 23, *D. (D.) imitans*, 220×. 24, *D. (D.) halli*, 220×.



Figs. 25–30. ♀ *Dermacentor* (*Dermacentor*) spp., left spiracular plates. 25, *D. latus*, 190×. 26, *D. albipictus*, 190×. 27, *D. hunteri*, 240×. 28, *D. occidentalis*, 240×. 29, *D. andersoni*, 190×; *D. variabilis*, 190×.



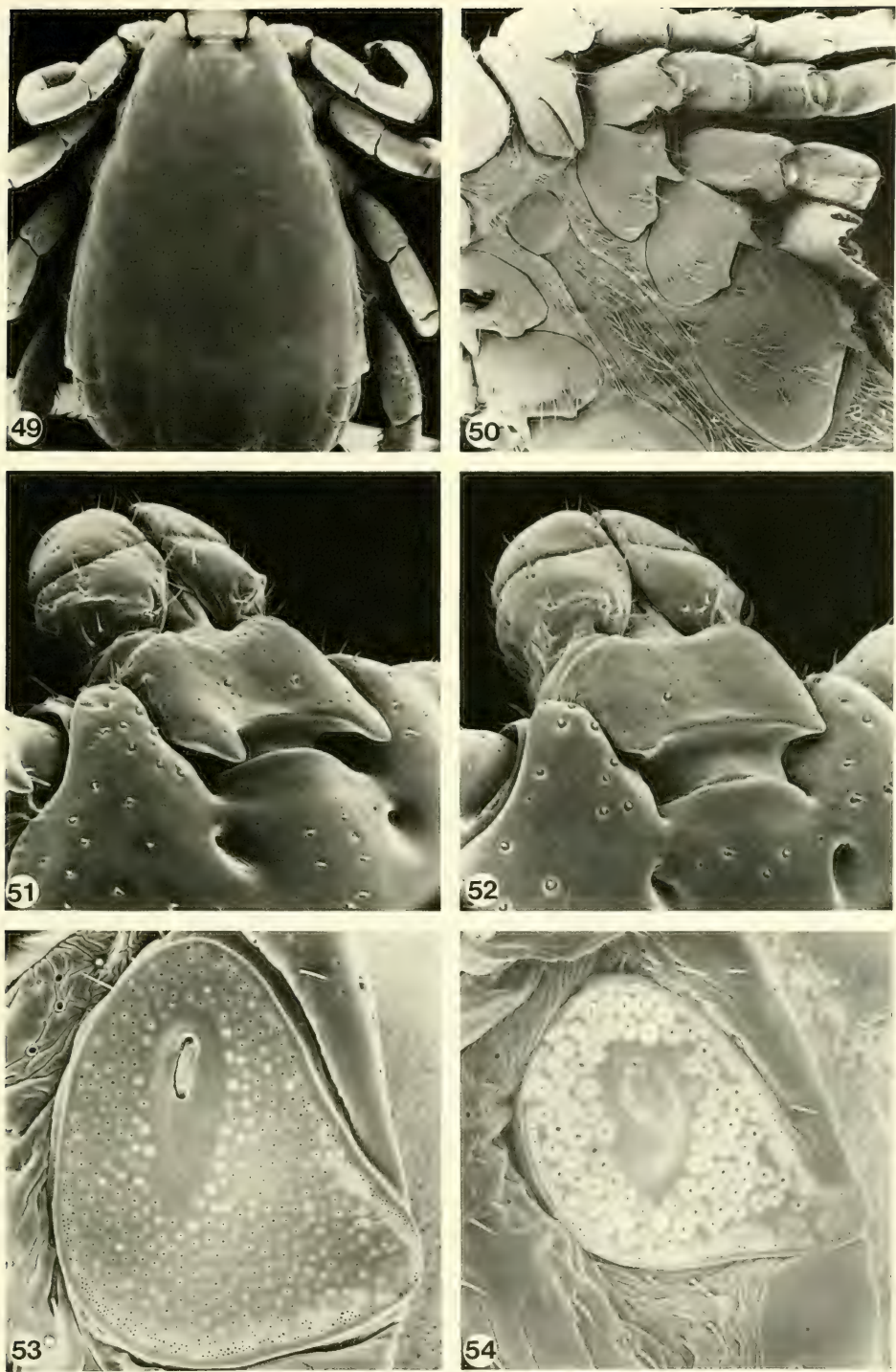
Figs. 31–36. ♂ *Dermacentor* spp. 31, *D. (Anocentor) nitens*, dorsum, 32×. 32, *D. (D.) hunteri*, dorsum, 21×. 33, *D. (D.) dispar*, coxae I–IV, 32×. 34, *D. (D.) dispar*, dorsum, 32×. 35, *D. (D.) dissimilis*, coxae I–IV, 74×. 36, *D. (D.) parumapertus*, coxae I–IV, 64×.



Figs. 37-42. ♂ *Dermacentor* (*Dermacentor*) spp. 37, *D. (D.) parumapertus*, dorsum, 32×. 38, *D. (D.) occidentalis*, dorsum, 21×. 39, *D. (D.) imitans*, coxae I-IV, 42×. 40, *D. (D.) halli*, coxae I-IV, 42×. 41, *D. (D.) imitans*, left spiracular plate, 212×. 42, *D. (D.) halli*, left spiracular plate, 212×.



Figs. 43–48. ♂ *Dermacentor* (*Dermacentor*) spp. 43, *D. (D.) imitans*, capitulum, dorsal view, 74×. 44, *D. (D.) halli*, capitulum, dorsal view; 74×. 45, *D. (D.) latus*, coxae I–IV, 32×. 46, *D. (D.) latus*, dorsum, 21×. 47, *D. (D.) hunteri*, left spiracular plate, 212×. 48, *D. (D.) occidentalis*, left spiracular plate, 212×.



Figs. 49-54. ♂ *Dermacentor* (*Dermacentor*) spp. 49, *D. (D.) albipictus*, dorsum, 21×. 50, *D. (D.) albipictus*, coxae I-IV, 64×. 51, *D. (D.) occidentalis*, showing elevated cornua, oblique view, 95×. 52, *D. (D.) andersoni*, showing nonelevated cornua, oblique view, 85×. 53, *D. (D.) variabilis*, left spiracular plate, 190×. 54, *D. (D.) andersoni*, left spiracular plate, 190×.

REPRODUCTIVE AND NESTING BIOLOGY OF
BEMBECEINUS NANUS STRENUUS (MICKEL)
(HYMENOPTERA, SPHECIDAE)

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Abstract. — A population of *Bembecinus nanus strenuus* was studied in a blowout among dunes near Roggen, Weld County, Colorado. Males fly over the emergence and nesting area in irregular patterns and respond to small, dark objects, including conspecifics, on the soil surface. Males intercept post-emergent females perching on the sand, some of which have already begun nesting, and copulation occurs, lasting several seconds. Little aggression between males was observed. Nests of females are unicellular, 9 to 16.5 cm deep, and are provisioned progressively with insects of three families of Homoptera (Cixiidae, Dictyopharidae, Cicadellidae). A comparative discussion of the reproductive biology of males and females of this species and *B. quinquespinosus* is included.

The major details of the biology of digger wasps of the genus *Bembecinus* are relatively well known (reviews in Evans, 1955, 1966). One obtains the impression that there is little behavioral variation among the species of this genus. Recently, we had an opportunity to study populations of two species that occur in abundance at localized sites in Weld County, Colorado. We have reported on one of these, *B. quinquespinosus* (Say), elsewhere (O'Neill and Evans, 1983; Evans et al., 1986). We take the opportunity here to report on the second species, *B. nanus strenuus* (Mickel), and to point out several differences in the biology of the two species. With respect to color, *B. nanus* is a monomorphic species, both sexes being black with narrow, pale bands on the abdomen. In contrast, *B. quinquespinosus* is polymorphic in the male sex, larger males being almost entirely yellow, small males (like the females) being black with pale bands; males of intermediate size are intermediate in coloration (Krombein and Willink, 1951; O'Neill and Evans, 1983).

There are no published reports of *B. nanus strenuus*, but Shappirio (1946) found an aggregation of the eastern subspecies, *B. nanus nanus* (Handlirsch), in Washington, D.C., and presented brief notes on the nest provisioning. The prey consisted of leafhoppers and a species of Fulgoroidea. It is probable that Bridwell's (1937) report of *B. moneduloides* (Smith) from Virginia also applies to *B. n. nanus*, the only species of the genus occurring in that area. Bridwell found a cocoon surrounded by the remains of 15 Homoptera of 8 species belonging to the families Cicadellidae, Membracidae, Cercopidae, Acanaloniidae, and Cixiidae. The use of

a variety of Homoptera is consistent with our observations of *B. n. strenuus* in Colorado.

Our studies were conducted in a blowout in sand dunes near Roggen, Colorado, where these wasps have been abundant at least since 1974. The wasps occupied a broad area, measuring about 5 by 12 m, on a gentle slope sparsely vegetated with grasses and scurfpea, *Psoralea lanceolata* Pursh. Studies of another digger wasp *Philanthus psyche* were conducted at this site (O'Neill, 1979, 1983), and, in fact, the nests of the two species were intermingled. *B. nanus strenuus* is active primarily through the month of July; our studies were made intermittently 6–30 July 1982–1985.

REPRODUCTIVE BEHAVIOR

During the early part of the day (0800–1300) up to several hundred males flew in irregular patterns several m long and 2–5 cm high, but rising to 30 cm to pass over plants. Males sometimes pursued other insects flying close to the ground, such as male Mutillidae. While individually marked males were found to remain for the most part within a few meters of the same site, there was no observed tendency for males to defend a specific area. Between flights males perched briefly on the ground, the duration of perches decreasing markedly as surface and air temperature increased during the day; surface temperature varied between 25° and 54°C during the activity period. There was a significant negative correlation between sand surface temperature (measured with a Model 870 Keithley digital thermocouple thermometer) and the duration of perches between patrolling flights ($r = -0.54$; $N = 146$; $P < 0.001$). On 8 July, 1984 at 1015, when the surface temperature reached 46°C, males began to perch between some flights on scurfpea plants rather than on the surface; by 1115, when the surface temperature had reached 54°C, males perched only on plants. In contrast to *B. quinquespinosus*, where only large males were active at high temperatures (O'Neill, unpublished data), the body size of males active (sampling without replacement) between surface temperatures of 26° and 52°C was not correlated with these temperatures ($r = -0.04$; $N = 100$; $P = 0.68$).

Males also interact frequently with conspecifics (or objects resembling the dark-colored conspecifics). They pounce upon various dark objects of about their own size on the sand. Pale, immature grasshoppers were abundant at the site, but generally elicited no response; however, males did occasionally drop onto darker colored grasshoppers, *Dactylotum bicolor* Thomas. In an effort to quantify the males' preference for darker colored objects, we prepared a series of small wooden cylinders, 15 mm long by 4 mm in diameter, painted with 6 colors of Testor's gloss enamel paints®. These were glued to a board 5 cm apart and parallel to one another; the board was placed on the sand with only the wooden cylinders exposed. Males flying over the area struck or landed upon the black cylinder significantly more often than on the other colors ($\chi^2_5 = 460.4$; $P < 0.0001$). The following is the frequency of responses to the six colors over one hour (0900 to 1000) on 9 July 1985: orange, 24; green, 9; white, 0; black, 125; yellow, 0; blue, 0.

In contrast, an identical series of observations undertaken on *B. quinquespinosus* on 16 July 1985, between 0900 and 1000, gave the following pattern of responses: orange, 11; green, 36; white, 1; black, 7; yellow, 6; blue, 0. Although this also represents a non-random pattern ($\chi^2_5 = 86.8$; $P < 0.001$), there was no tendency

for a biased response towards black. The potential significance of this will be discussed later.

On 15 occasions we saw males of *B. nanus* descend upon females perched upon the sand surface; in 7 of these instances, this resulted in matings lasting only 3 to 5 seconds. Males sometimes descended upon females working at nest entrances, and on one occasion apparently mated successfully with such a female, although on 8 others the females rejected the male, usually with a vigorous struggle, after contact was made. Other females flew off as patrolling males approached them.

Males displayed little overt aggression toward one another. They frequently pounced upon perched males during patrolling flights, but the duration and form of these interactions suggest that they were misdirected copulation attempts, rather than aggressive interactions. Flying males also approached one another within several cm, briefly hovering face-to-face without making contact. Only one male was present in 87% of 15 observed copulation attempts and mating was usually completed *in situ* without interference. In the two cases in which more than one male was present, the interactions were short-lived and not of the intensity usually observed in *B. quinquespinosus* (O'Neill and Evans, 1983). Once two males attempted copulation at the same time, but the larger of the two displaced the smaller and mated with the female. On another occasion, 4 males formed a cluster around a female; one emerged with the female, but had difficulty flying with the female, which was larger, and mated only a short distance away. Thus, the mating tactics of *B. nanus* are generally in the form of a scramble competition, although interference competition occasionally occurs.

NESTING BEHAVIOR

Females nested in the same area from which they had emerged and over which the males patrolled. Sand is removed from the burrow with simultaneous movements of the forelegs and allowed to form a small mound at the entrance. From time to time, the female backs across the mound and moves forward in a somewhat zig-zag pattern, partially dispersing the sand. Burrows are oblique, 16–25 cm long, reaching a cell at its terminus at a depth of 9–16.5 cm (mean = 13.5, N = 12). Burrows are straight or nearly so, and nests are unicellular. As in other species of the genus, the egg is laid in the empty cell on top of several grains of sand, sloping away from the entrance, and prey are brought in progressively over the next several days. Nests in this area were well-dispersed, usually at least 30 cm apart. At one site, measuring 60 cm², near the center of the nesting area, we sifted the soil, but found only 4 cocoons.

Combined prey from several nests consisted of a variety of Homoptera, as follows:

Cixiidae: *Oecleus excavatus* Ball, 2 adults

Dictyopharidae: *Scolops maculosus* Ball, 9 adults

Scolops sp., 34 immatures

Cicadellidae: 16 adults of 9 species; also 10 immatures

Cicadellinae

Carneacephala sp., probably *gillettei* Ball, 1 male

Cuerna striata (Walker), 2 females, 2 males

Draeculacephala sp., 1 female

Agalliinae

Aceratagallia sp., probably *sanguinalenta* (Prov.), 2 females

Hecalinae

Dicyphonia ornata (Baker), 2 females

Dectocephalinae

Acinopterus viridis Ball, 2 females, 1 male

Athysanella wilburi Ball and Beamer, 1 male

Flexamia inflata Osborn and Ball, 1 female

Mesamia sp., probably *nigridorsum* (Ball), 1 female

DISCUSSION

The two species of *Bembecinus* that we have studied in northeastern Colorado contrast markedly with respect to male mating strategies. In *B. quinquespinosus* the male color polymorphism correlates with alternative mating tactics. The extensively yellow males compete vigorously before and after digging emerging females from the soil; the smaller, darker males are generally found to patrol the area adjacent to the emergence area and attempt to mate with females that elude attempts of the larger males (O'Neill and Evans, 1983 and unpublished data). The latter tactic is essentially identical in form, though not in location, to the only mating tactic that we identified for *B. nanus strenuus*; this form of male mating activity has been commonly observed in the subfamily Nyssoninae (Evans, 1966). The fact that males of *B. nanus* search for black "objects" upon the sand, while males of *B. quinquespinosus* respond to the presence of groups of digging conspecific males which are yellow may explain the species differences in response to our colored cylinders in the observations described above. Males of the former species may thus be reacting to the presence of a potential mate (black), while those of the latter are responding to males that gather at the potential emergence site of a female. Presumably the green paint we used had reflectance properties similar to the greenish-yellow of the larger males.

The two species also differ with respect to the degree of sexual size dimorphism, another trait that appears to be related to differences in male mating tactics. While in *B. quinquespinosus* males and females have the same mean size and size range (O'Neill and Evans, 1983), females of *B. nanus strenuus* (mean head width = 2.60 mm, SD = 0.20, N = 47) are significantly larger than males on average (mean male head width = 2.37, SD = 0.15, N = 123; *t*-test, $t_{163} = 9.81$, $P < 0.001$). The latter is typical of digger wasps in general (O'Neill, 1985). In the former species, the result is that the large yellow males in the emergence area are usually larger than emerging females. This allows them to more easily lift and carry females in flight in order to escape the usually intense competition (O'Neill and Evans, 1983 and unpublished data). On the other hand, since males of *B. nanus* usually find females without conspecific male competitors present, carrying the female away from the emergence area would usually accrue little advantage in terms of increased mating success. Thus, in contrast to *B. quinquespinosus*, there may be little selection pressure for larger relative body size in *B. nanus*.

In *B. quinquespinosus*, females nest at a different site each year, while maintaining the integrity of their dense aggregations. These sites may be 100 m apart in consecutive years. We have suggested elsewhere that this movement is a re-

sponse to harassment by males of females attempting to nest in the emergence area while searching males are still present (Evans et al., 1986). On the other hand, the population of *B. nanus strenuus* we studied has nested in the same place for several consecutive years, presumably a reflection of the more diffuse nests and the lower male density, resulting in less harassment of nesting females.

In contrast to the diversity of prey used by *B. nanus strenuus*, the population of *B. quinquespinosus* we studied (O'Neill and Evans, 1983; Evans et al., 1986) preyed exclusively upon Cicadellidae of two species, *Cuerna striata* (Walker), 121 adults, and *Amphigonalia* sp. near *gothica* (Signoret), 13 adults (both Cicadellinae), plus 623 immature Cicadellidae (probably of these same two species). Nests were similar to those of *B. nanus strenuus* though dug in much coarser sandy gravel; cell depth varied from 8 to 12 cm (mean = 9.9, N = 8). Neither species makes accessory burrows as described for certain Australian species (Evans and Matthews, 1971). Nest density differs greatly in the two species, nests of *B. quinquespinosus* often being only 5–10 cm apart, such that burrows are closely adjacent and may intersect.

It appears that most species of *Bembecinus* employ Homoptera of diverse groups; thus exclusive use of Cicadellidae may be a specialization. Other published records for *B. quinquespinosus* (under the name *godmani*) confirm its restriction to Cicadellidae (review by Evans, 1955). Only the South American species *B. agilis* is also reported to specialize on Cicadellidae (Richards, 1937, under the name *cingulatus*). On the other hand, not only *nanus*, but three European, three Australian, and three Asiatic species are known to each use a variety of homopteran families (Evans, 1955; Evans and Matthews, 1971; Krombein, 1984). Two anomalous, turret-building South African species use both Homoptera and Diptera as prey (Gess, 1975).

It seems safe to categorize *B. nanus* as a relatively generalized member of the genus with respect to its reproductive behavior; it possesses traits typical of most *Bembecinus* in particular and many nyssonines in general. On the other hand, *B. quinquespinosus* exhibits many derived behavioral and morphological traits: the females specialize on cicadellid leafhoppers and move their nesting area each year, the males have a unique color polymorphism, are the same average size as females, and possess rudimentary rake spines on their forelegs that may aid in digging for females (O'Neill and Evans, 1983). It must be pointed out that these differences are based upon one population of each species studied at different localities in Colorado. Other published observations (Evans, 1955) on these species do not contradict these statements, but at this point it would be premature to maintain that species differences are consistent throughout their respective ranges, particularly with regard to relatively labile behavioral traits.

ACKNOWLEDGMENTS

We thank Paul H. Freytag, of the University of Kentucky, and H. Derrick Blocker, of Kansas State University, for identifying the Cicadellidae; also Stephen W. Wilson, of Central Missouri State University, for identifying the *Scolops*. Ruth O'Neill provided assistance with the field work.

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NOTES ON THE *Aedes* (*Diceromyia*) *furcifer* GROUP, WITH A DESCRIPTION OF A NEW SPECIES (DIPTERA: CULICIDAE)¹

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Abstract. — The larva and pupa and both sexes of the adult of *Aedes* (*Diceromyia*) *cordellieri* n. sp. from Ivory Coast are described and illustrated. *Aedes cordellieri* is most closely related to *Aedes* (*Diceromyia*) *taylori* Edwards. Detailed description and illustrations of the male genitalia of *Ae. taylori* are also presented. Diagnostic characters for separating the *Aedes furcifer* group from other *Diceromyia* are provided. The distribution of *Ae. cordellieri* is based on examined specimens.

Recent field work in Ivory Coast produced a reared series of a third species of the *Aedes* (*Diceromyia*) *furcifer* group, confirming my earlier observations of an additional species from the limited material then available in our collections. Although members of this species group are important as vectors of certain arboviruses, there remains some confusion in distinguishing among the species. Thus, the purpose of this paper is to describe the new species, with emphasis on characters to distinguish it from its sister species, *Aedes taylori* Edwards, and to provide other clarifying comments on the species group.

MATERIALS AND METHODS

This study is based on specimens that were collected or otherwise acquired by the Medical Entomology Project (MEP) and the Systematics of *Aedes* Mosquitoes Project (SAMP), Department of Entomology, National Museum of Natural History, Smithsonian Institution (USNM). Distribution records are listed in the following order and format: country names are in capital letters, administrative divisions, where known, are in italics, and place names have the first letter capitalized.

The terminology follows that of Harbach and Knight (1980), with the exception of "tarsal claws," which is retained for "unguis." The venational terms follow those of Belkin (1962).

The *Aedes* (*Diceromyia*) *furcifer* group

Included species. — The *Aedes* (*Diceromyia*) *furcifer* group in the Afrotropical Region consists of at least three species. These include *Aedes furcifer* (Edwards),

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Ae. taylori Edwards, and the new species, *Aedes cordellieri*, described here. The last two species form the *taylori* complex.

Diagnosis.—The *furcifer* group can be distinguished from other *Diceromyia* by the following combination of characters: (1) proboscis with a distinct white band; (2) erect, forked scales numerous, not restricted to occiput; (3) acrostichal, dorsocentral and prescutellar setae well developed; (4) paratergite with pale scales; (5) lower mesepimeral setae present; (6) scutellum with broad scales on all lobes; (7) wing with broad dark scales mixed with broad white scales on all veins; and (8) femora, tibiae and tarsomeres 1 sprinkled with pale scales.

Medical importance.—Members of the *furcifer* group have been incriminated as vectors of Yellow Fever in Africa (Lewis, 1943, in the Nuba mountains, Sudan [as Anglo-Egyptian Sudan]; Cordellier et al., 1974, in Burkina Faso [as Upper Volta] and Mali; Port and Wilkes, 1979, in Gambia), and of Chikungunya (McIntosh et al., 1964, and Paterson and McIntosh, 1964, in Zimbabwe [as Southern Rhodesia]; McIntosh et al., 1977, and Jupp, 1980, in South Africa). The following viruses have also been isolated from members of the *furcifer* group: yellow fever, chikungunya, Zika, Bouboui and Bunyamwera in Senegal (Cornet et al., 1978, 1979) and yellow fever in Burkina Faso [as Upper Volta] (Baudon et al., 1984).

Discussion.—*Aedes furcifer* and *Ae. taylori* have been treated as two species, usually found sympatrically, that are difficult to separate morphologically. The difficulty in separating females of *Ae. furcifer* from *Ae. taylori* was first reported by Lewis (1943: 72), who stated that, “The distinguishing character of the females given by Edwards (1941)—the degree of speckling of the abdominal tergites—proves to be so variable in Sudan specimens of *Ae. furcifer* that the two species cannot always be differentiated In the following observations these two very similar species are treated together.” Since then, the so-called “*Aedes furcifer-taylori* group” has been used for these two species of mosquitoes, which have not always been differentiated by workers conducting studies on them (Haddow, 1961; McIntosh et al., 1964; Paterson and McIntosh, 1964; Cordellier et al., 1974; Cornet et al., 1978, 1979; Port and Wilkes, 1979; Germain et al., 1980; Jupp, 1980). The difficulty in distinguishing females of *Ae. furcifer* from *Ae. taylori* was also noted by Lewis (1945: 12), Bailey (1947: 39), Mattingly (1949: 388), Muspratt (1955: 174), Van Someren et al. (1955: 481), Haddow (1961: 323), Hamon (1963: 106), Cornet et al. (1978: 1450; 1979: 157), Port and Wilkes (1979: 343) and Germain et al. (1980: 11).

Edwards (1936:55) described *Ae. taylori* from specimens collected in Gadau, Nigeria, and mentioned that it “resembles *furcifer* . . . but differs from *furcifer* in having no scattered pale scales on the dark parts of the abdomen.” In a later treatment of *Ae. taylori*, Edwards (1941: 216) mentioned that it is “closely related to *A. furcifer* . . . except that there are no (or at most extremely few) scattered yellowish scales on the abdominal tergites.” The variation noted in the character Edwards used to differentiate *Ae. taylori* from *Ae. furcifer* was attributed to intraspecific variation. Edwards did not realize that his concept of *Ae. taylori* included two species and that he was dealing with interspecific variation.

It is now evident from using couplet 4 of Edwards’ key (1941: 214) that *Ae. cordellieri* has apparently been misidentified as *furcifer*, as the “abdomen speckled dorsally” is a character found in both *furcifer* and *cordellieri*. On the other hand, the second half of couplet 4, “abdomen not speckled dorsally” is a reliable specific

character for *taylori* and can be used to separate *taylori* from either *furcifer* or *cordellieri*. Males of *Ae. cordellieri* have been misidentified as *taylori* because the character "without the tuft of setae on the tips of the gonocoxites," which has been used to differentiate *Ae. taylori* from *Ae. furcifer* since Edwards (1936), is also found in *Ae. cordellieri*. For example, I have found that all male specimens from Kenya, Tanzania, Uganda and South Africa in the USNM collection were misidentified as *taylori*. It must be noted that the character "without the tuft of setae on the tips of the gonocoxites" cannot be used as the specific diagnostic character for identifying *taylori* Edwards, but it is the character for separating the *taylori* complex (*taylori* and *cordellieri*) from the *furcifer* complex (*furcifer* and perhaps others).

The diagnostic value of the ornamentation on the abdominal sternites, as mentioned by Ferrara et al. (1984: 182), can only be used for distinguishing between *Ae. furcifer* and *Ae. taylori*, but cannot be used for distinguishing between *Ae. furcifer* and *Ae. cordellieri* (see descriptions under female and male of *Ae. cordellieri*). Therefore, the key given by Ferrara et al. (1984) is inadequate for distinguishing between *Ae. furcifer* and *Ae. taylori*.

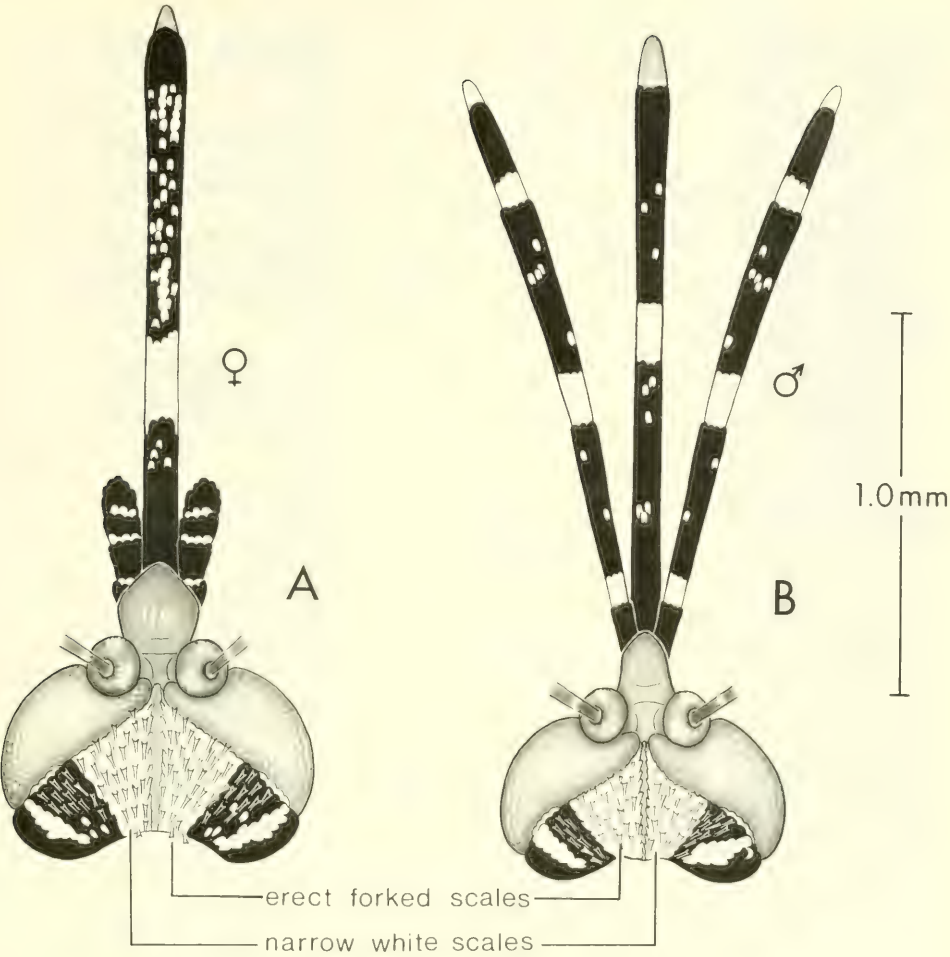
Adults of *Ae. cordellieri* n. sp. and *Ae. furcifer* (Edwards) run to the first half of couplet 4 in Edwards' (1941) key to Ethiopian species of subgenus *Diceromyia*. The two species can be distinguished as follows: terga II–VII with pale scales scattered on apicolateral and dorsomedian areas (*furcifer*); terga II–VII with yellowish scales scattered on apicolateral areas only, no scattered pale or yellowish scales on dorsomedian areas (*cordellieri* n. sp.).

In view of the past taxonomic confusion in the *furcifer* group and its involvement in the epidemiology of arboviruses in Africa, it is desirable to describe the new species and to provide also a detailed description and illustrations of the male genitalia of *Ae. taylori*. Results of further investigations on the *furcifer* group will be published in due course.

Aedes (Diceromyia) cordellieri Huang, NEW SPECIES

Figs. 1, 2, 3A, 4, 5

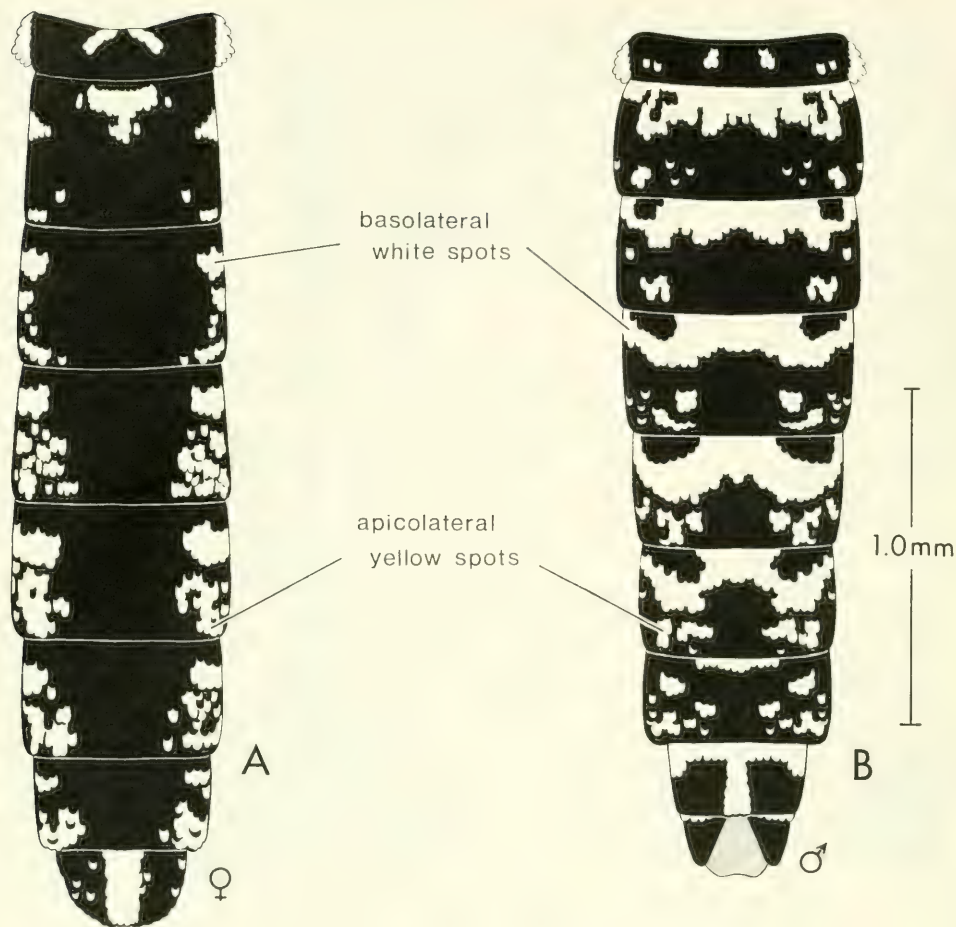
Female.—*Head* (Fig. 1A): Proboscis dark scaled, with white scales scattered and with a distinct white band near middle, about as long as forefemur; maxillary palpus 0.23–0.25 length of proboscis, dark, with a white band at base of palpomeres 3, 4 and a white band at the middle of palpomere 4, sometimes with few white scales scattered on palpomere 4 instead of a white band at middle, or sometimes without scattered white scales; pedicel covered with some white scales on dorsal and ventral areas of inner side; antenna with a small patch of white scales on mesal surface of flagellomere 1; clypeus with a few white scales; erect forked scales, numerous, not restricted to occiput, mainly white, some dark ones on sides; vertex with a large median area of narrow white scales, with broad dark scales on each side interrupted by lateral stripe of broad white scales, followed ventrally by a patch of broad white scales. *Thorax*: Scutum with narrow pale yellow scales, and a distinct patch of narrow dark scales on fossal area, a broad longitudinal stripe of narrow dark scales on posterior dorsocentral area, a lateral patch of narrow dark scales on each side just above the paratergite; prescutellar area with some narrow pale yellow scales; acrostichal, dorsocentral and prescutellar setae well developed; scutellum with broad pale yellow scales on all lobes



Aedes (Diceromyia) cordellieri n. sp.

Fig. 1. *Aedes (Diceromyia) cordellieri*. A, Dorsal aspect of the allotype female head. B, Dorsal aspect of the holotype male head.

and a few narrow ones at base of midlobe, with a few broad dark scales at apex of all lobes; antepronotum with broad and narrow pale yellow scales; postpronotum with broad dark scales and some broad pale yellow scales in middle and ventrally; paratergite with pale yellow scales; postspiracular area with few pale yellow scales; hypostigmal area with small patch of pale yellow scales; patches of broad pale yellow scales on propleuron, subspiracular area, upper and lower portions of mesokatepisternum, and on mesepimeron; lower mesepimeron usually with 2 (1–3) seta; metameron and mesopostnotum bare. *Wing*: With broad dark scales mixed with broad white scales on all veins; cell R_{2+3} 2.2–2.5 length of R_{2+3} . *Halter*: With dark scales. *Legs*: Coxae with patches of pale yellow scales; yellow



Aedes (Diceromyia) cordellieri n. sp.

Fig. 2. *Aedes (Diceromyia) cordellieri*. A, Dorsal aspect of the allotype female abdomen. B, Dorsal aspect of the holotype male abdomen.

knee-spot present on femora; femora, tibiae, and tarsomeres 1 sprinkled with pale yellow scales; foretarsus with a basal white band on tarsomeres 1-3; midtarsus with a basal white band on tarsomeres 1-4; hindtarsus with a basal white band on tarsomeres 1-5; fore- and midlegs with tarsal claws equal, all toothed; hindleg with tarsal claws equal, both simple. *Abdomen* (Fig. 2A): Tergum I with white scales on laterotergite, with a few white scales on basomedian area; tergum II with a basomedian white band or patch and basolateral white spots which do not connect with the basomedian white band or patch; terga III-VII each with basolateral white spots which are turned dorsomesally; terga II-VII each with yellow scales sprinkled on apicolateral area, those on terga III-VII often form distinct yellow patches; terga III-VII usually each with dorsomedian area dark, sometimes with a few white scales on basomedian area; tergum VIII with a median longitudinal white stripe; sterna II-VI each with a basal white band and with white

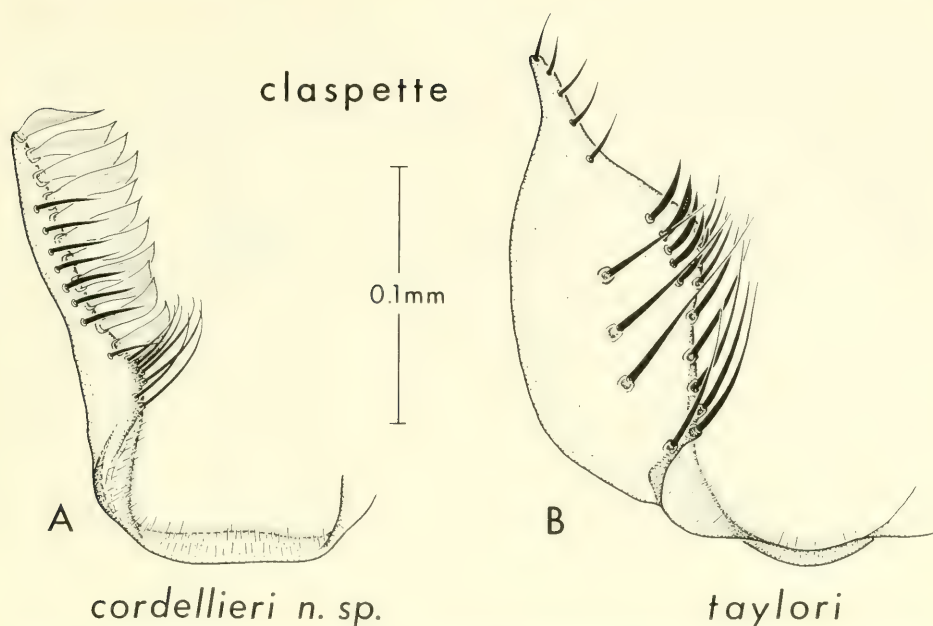
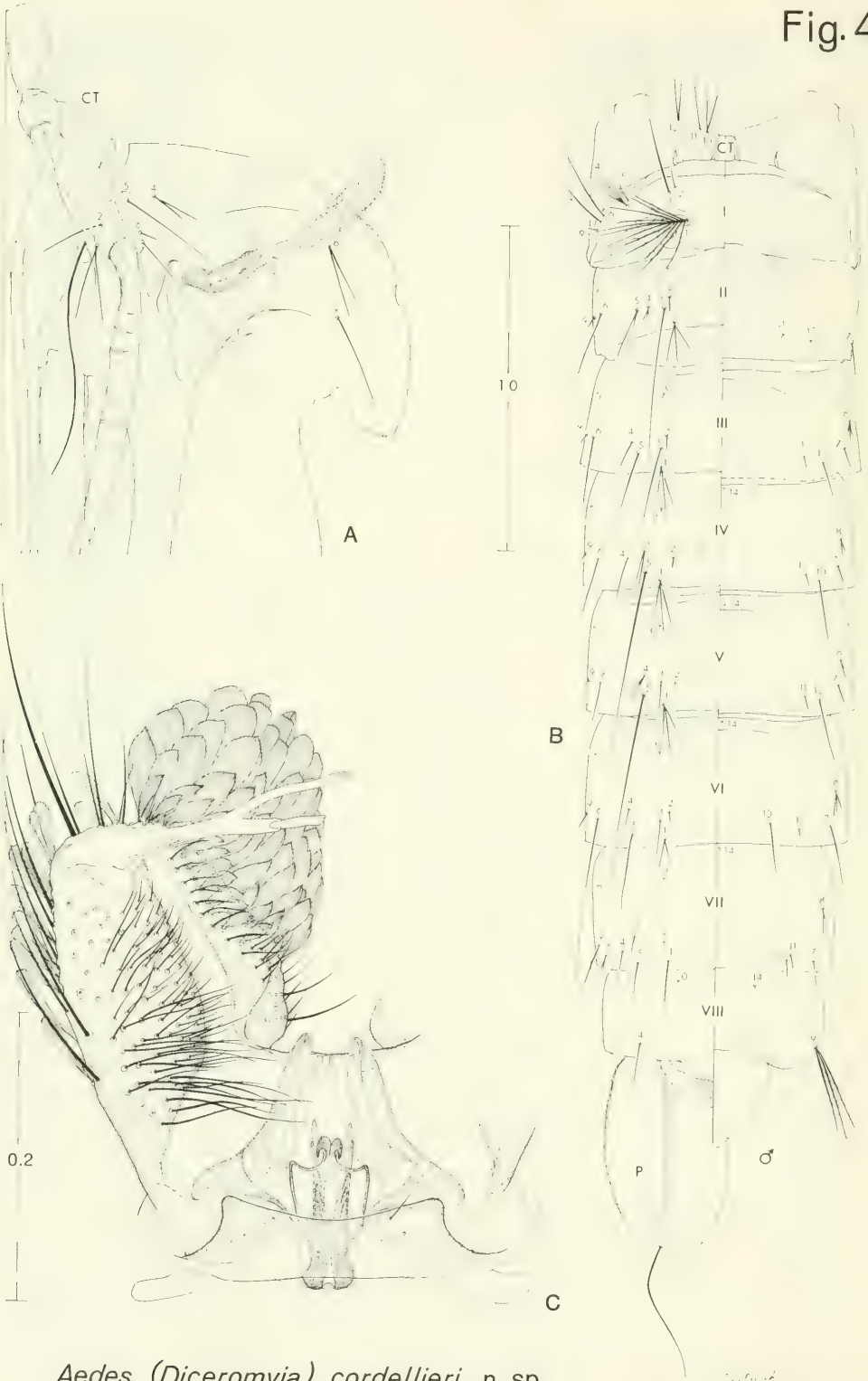


Fig. 3. *Aedes* (*Diceromyia*) *cordellieri*. A, Dorsal aspect of the claspette of the male genitalia; *Aedes* (*Diceromyia*) *taylora*. B, Dorsal aspect of the claspette of the male genitalia.

scales scattered on remainder; segment VIII not completely retracted. *Genitalia*: Apical margin of sternum VIII without a median notch and without conspicuous rounded lateral lobes; insula longer than wide, with minute setae and with 4 larger setae on apical 0.25; apical margin of tergum IX with a well developed lateral lobe, with 1–2 setae; apical margin of postgenital plate with or without a small notch; cercus short and broad; 3 spermathecae, one larger than the other 2.

Male.—Essentially as in the female, differing in the following sexual characters: *Head* (Fig. 1B): Maxillary palpus, shorter than proboscis, 0.90–0.92 length of proboscis, dark, with a white band at base of palpomeres 2–4 and with white scales scattered on palpomeres 2, 3; palpomere 4 very short and with a few short stiff setae at apex; palpomere 5 minute, with all white scales; antenna plumose, shorter than proboscis. *Wing*: Cell R_2 1.4–1.7 length of R_{2+3} . *Legs*: Midtarsus with a basal white band on tarsomeres 1–3; fore- and midlegs with tarsal claws unequal, both toothed. *Abdomen* (Fig. 2B): Terga II–VI each with a basomedian white band and basolateral white spots which are dorsomesally turned and connect with the basomedian white band; tergum VII with a basomedian white band and basolateral white spots which do not connect with the basomedian white band; terga I–VII each with yellow scales sprinkled on apicolateral area, those on terga II–VII often form distinct yellow patches; sterna II–VII each with a basal white band and without white scales scattered on remainder, sometimes with a few white scales scattered on sterna II–IV. *Genitalia* (Figs. 3A, 4C): Gonocoxite short and broad, about 1.8 as long as wide (width measured 0.5 from base), truncate at apex, without a projecting lobe bearing numerous long setae on apicomeral area, scales restricted to dorsolateral, lateral and ventral surfaces, with dense scales on mesal margin of ventral surface, with setae scattered on dorsomesal surface,

Fig. 4



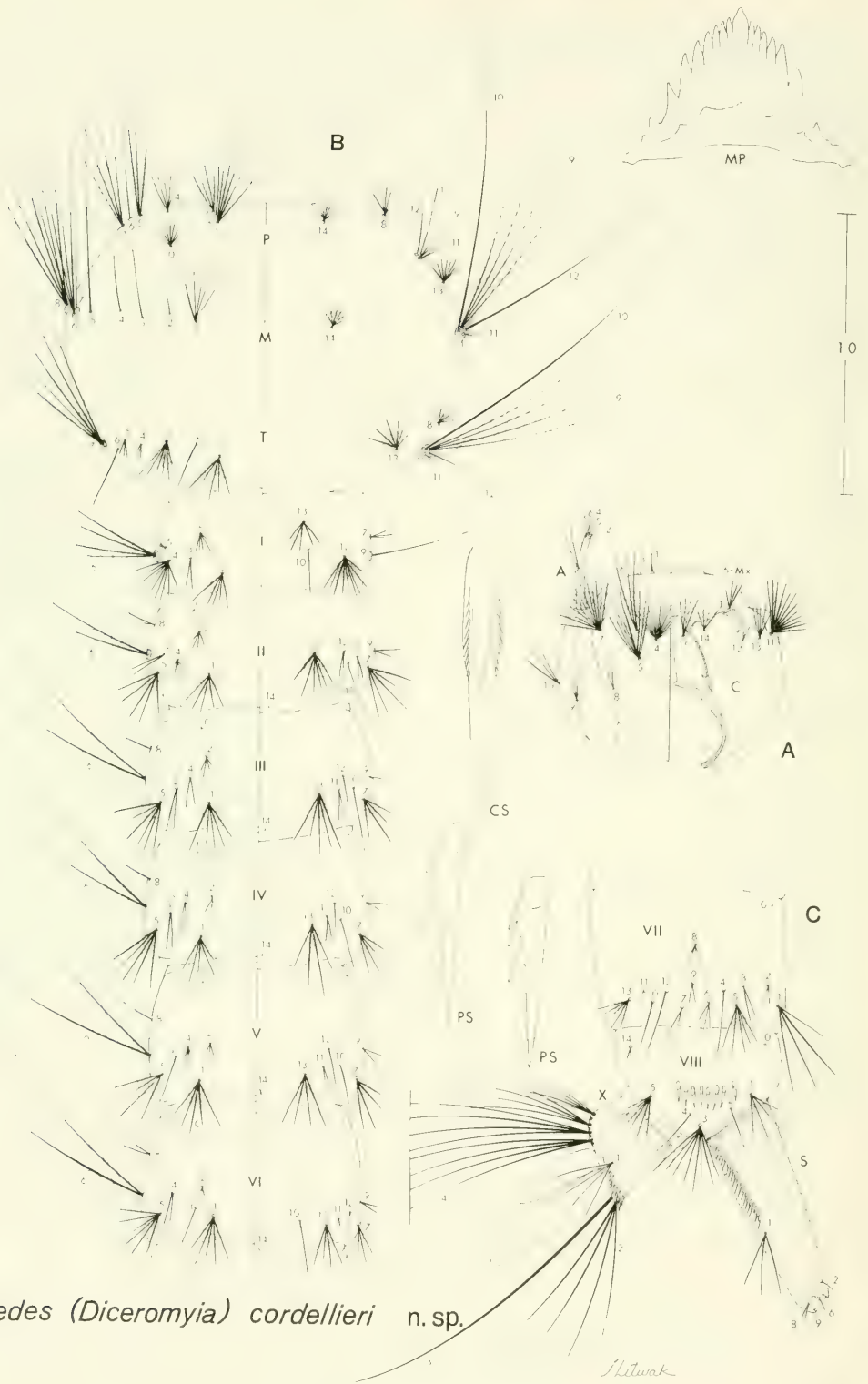
Aedes (Diceromyia) cordellieri n. sp.

mesal surface membranous; claspette long, reaching to 0.8 of gonocoxite, with a row of scales along the mesal margin from apex to basomesal corner and with a row of short setae along the row of scales, followed by a few long, curved setae along the mesal margin of basal part, and without distinct, stout, long, pointed spines on median area of slightly expanded basal part; gonostylus elongate, slender, about 0.85 length of gonocoxite, bifurcate at about 0.63 from base, upper arm longer than the lower one, with a blunt, stout claw process apically on the shorter one; aedeagus with strongly toothed lateral plates; paraproct without apical teeth, cercal setae absent; apical margin of tergum IX slightly concave medially, with 3 (2–4) setae on each side; sternum IX with 11–12 setae.

Pupa (Figs. 4A, 4B).—*Cephalothorax*: Trumpet 5.0–6.0 as long as wide (width measured 0.5 from base); seta 1-CT usually double (1–3); 2-CT single; 3-CT usually single (1–2), long, longer than 2-CT; 4-CT usually double (1–3); 5-CT single, long; 6-CT single, short; 7-CT usually single (1–2), long, longer than 6-CT; 8-CT usually double (2–3); 9-CT single; 10-CT usually double (2–3), caudomesad of 11-CT; 11-CT single; 12-CT usually double (1–3). *Abdomen*: Seta 1-I well developed, usually with 12 (12–17) plumose branches; 2-I single, short; 3-I single, long; seta 1-II usually with 3 branches (2–5); 3-II, III usually single (1–2); 1-III, IV usually with 3 branches (2–4); 5-IV, V single, long, reaching beyond posterior margin of following segment; seta 6-VI single, long, reaching beyond posterior margin of following segment; seta 9-I-VI small, single, simple; 9-VII usually single (1–2) and barbed; 9-VII, VIII much longer and stouter than 9-I-VI; 9-VIII usually with 3 branches (3–6) and barbed. *Paddle*: Oval, about 1.6 as long as wide; with small denticles on outer margin and on apical 0.28–0.30 of inner margin; without fringe of long hair-like spicules; apex rounded; seta 1-P single, long.

Larva (Fig. 5).—*Head*: Antenna with spicules; seta 1-A inserted in apical 0.5 of shaft, usually double (2–3); inner mouthbrushes not apically pectinate; seta 4-C well developed, usually with 16 branches (13–22), caudomesad of 6-C; 5-C usually with 8 branches (7–11), barbed; 6-C usually with 3 branches (2–4), barbed; 7-C usually with 12 branches (11–16), barbed; 8-C usually double (1–2); 9-C usually with 4 branches (3–5); 10-C usually with 3 branches (2–4); 11-C usually with 12 branches (12–14), barbed; 12-C usually with 4 branches (4–5); 13-C usually with 5 branches (3–5); 14-C usually with 4 branches (3–6); 15-C usually with 4 branches (3–5); mentum usually with 8 or 9 (7–10) teeth on each side of central tooth, with outer 4–5 teeth widely spaced. *Thorax*: Seta 1-P usually with 5 branches (4–6), barbed; 2-P single; 3-P usually with 4 branches (4–6), barbed; 4-P usually with 5 branches (4–5); 5-P usually with 3 branches (2–4), barbed; 6-P single; 7-P usually with 4 branches (2–6), barbed; 9-P usually double (2–4); 11-P double; 5,7-M single; 6-M usually with 4 branches (4–5), barbed; 8-M usually with 5 branches (3–5), barbed; 9-M usually with 4 branches (4–5), barbed; 10,12-M single, long, and stout; 11-M double, small; 7-T usually with 5 branches (3–7); 9-T usually with 4 branches (4–5), barbed; 10,11-T similar to those on mesothorax; 12-T much reduced, single and simple; basal spine of meso- and metapleural setae long,

Fig. 4. *Aedes (Diceromyia) cordellieri*. A, Dorsolateral aspect of the cephalothorax of the male pupa. B, Dorsal and ventral aspects of the metathorax and abdomen of the male pupa. C, Tergal aspect of the male genitalia.



Aedes (Diceromyia) cordellieri n. sp.

apically pointed. *Abdomen*: Seta 6-I usually with 4 branches (4–6), barbed; 7-I usually single (1–2); 6-II usually double (2–4), barbed; 7-II usually with 5 branches (4–6), barbed; 6-III–VI double, barbed; 1-VII usually with 4 branches (4–5); 2-VII usually double (2–3); 2-VIII distant from 1-VIII; 1-VIII usually with 4 branches (3–5), barbed; 3-VIII usually with 8 branches (7–9), barbed; 5-VIII usually with 6 branches (5–7), barbed; 2,4-VIII single; comb of VIII usually with 8 (6–10) scales in a row, each scale with fine basal lateral fringe; segment X with saddle incomplete, marginal spicules conspicuous; seta 1-X usually with 4 branches (3–5); 2-X usually with 4 branches (4–5); 3-X single; 4-X with 4 pairs of setae of grid, each seta usually with 3 or 4 branches (2–5); no precratal tufts; anal papillae sausage-like, dorsal pair longer than ventral pair. *Siphon*: About 2.5–3.8 as long as wide 0.5 from base, acus absent; usually with 19 (13–26) pecten spines, extending from base to 0.50–0.57 the length of siphon each spine usually with 2–3 basal denticles (1–4); seta 1-S with 3–4 branches, usually inserted beyond apical pecten spine and in 0.56–0.64 from base.

Type data.—Holotype ♂ (SAMP Acc. 1138, IV 380-16) with associated larval and pupal skins on slide, with genitalia on slide (85/314), Dezidougou, M'Bahiakro, *Centre Département*, IVORY COAST, reared from eggs collected from a ♀, biting man, at the ORSTOM study tower, 20 m above ground level, between 1730–1930 h, June 13, 1985, Huang and Pecor [USNM]. Allotype ♀ (SAMP Acc. 1138, IV 380-23) with associated larval and pupal skins on slide, same data as holotype [USNM]. Paratypes: 16 ♂, 11 ♀ and 3 4th instar larvae as follows, (SAMP Acc. 1138): 4 ♂ (IV 380-17, 18, 21, 24) with associated larval and pupal skins on slides, with genitalia on slides (85/192, 85/315, 85/316, 85/317) and 2 ♀ (IV 380-30, 31) with associated larval and pupal skins on slides, with genitalia on slides (85/319, 85/320), same data as holotype [USNM]; 2 ♂ (IV 380-11, 100) with associated pupal skins on slides, with genitalia on slides (85/191, 85/193), same data as holotype [USNM]; 1 ♂ (IV 380-102) with genitalia on slide (85/194) and 2 ♀ (IV 380-28, 101) with genitalia on slides (85/318, 85/195), same data as holotype [USNM]; 5 ♂ (IV 380-19, 20, 26, 33, 35) and 4 ♀ (IV 380-12, 14, 29, 34) with associated larval and pupal skins on slides, same data as holotype [USNM]; 1 ♂ (IV 380-10) with associated pupal skin on slide, same data as holotype [USNM]; 1 ♂ (IV 380-15) and 1 ♀ (IV 380-13) with associated larval and pupal skins on slides [ORSTOM]; 1 ♂ (IV 380-25) and 1 ♀ (IV 380-32) with associated larval and pupal skins on slides (Division of Vector-Borne Diseases, Ministry of Health, Nairobi, Kenya) [DVBD]; 1 ♂ (IV 380-22) and 1 ♀ (IV 380-27) with associated larval and pupal skins on slides [BM]; 3 4th instar larvae (IV 380) [USNM]; same data as holotype.

Other material examined.—IVORY COAST. *Centre Département*: M'Bahiakro: Dezidougou (7°44'N, 4°16'W), May 20, 1985, B. Bouchite, (SAMP Acc. 1138), 6 ♂ (IV 166), 3 ♀ (IV 166), 3 ♂ gen. (85/143, 85/144, 85/145), 2 ♀ gen. (85/159, 85/160) [USNM]; same data except May 22, 1985, 1 ♂ (IV 172), 1 ♂ gen. (85/146)

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Fig. 5. *Aedes (Diceromyia) cordellieri*. A, Dorsal and ventral aspects of the head of the fourth instar larva. B, Dorsal and ventral aspects of the thorax and abdomen of the fourth instar larva. C, Lateral aspect of the terminal abdominal segments of the fourth instar larva.

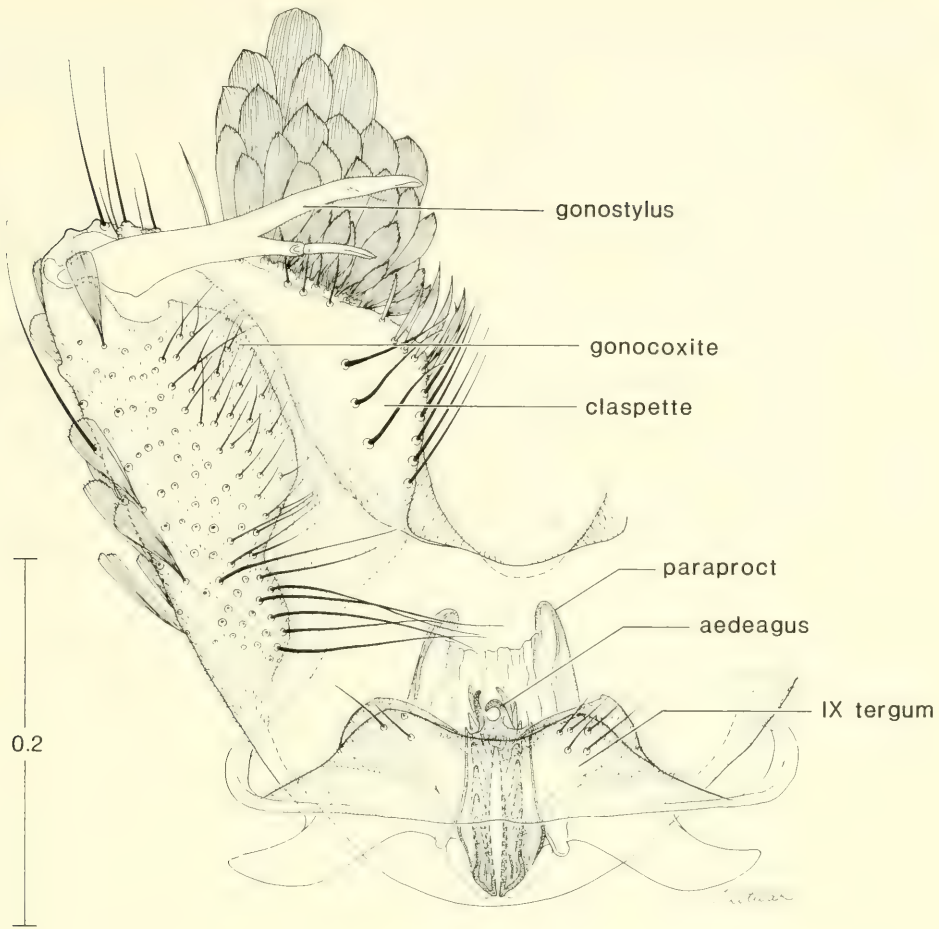
[USNM]; same data except Jun. 12, 1985, 1 ♂ (IV 376) [USNM]; same data except Jun. 13, 1985, 1 ♂ (IV 379), 1 ♀ (IV 380), 1 ♀ (IV 381) [USNM]; same data except Jun. 14, 1985, 3 ♂ (IV 384) [USNM]; Km 2, Jun. 14, 1985, B. Bouchite, (SEAMP Acc. 1138), 1 ♂ (IV 385) [USNM]. KENYA. *Coast Region*: Gede (3°18'S, 40°01'E), Apr. 1951, (SEAMP Acc. 111), 1 ♂, 1 ♂ gen. (83/459) [USNM]; *Rift Valley Region*: Kerio Valley (0°45'N, 35°35'E), Apr. 1958, W. E. Graunger, (SEAMP Acc. 111), 1 ♂, 1 ♂ gen. (79/245) [USNM]. TANZANIA (Tanganyika). *Mwanza Region*: Mwanza (2°31'S, 32°54'E), 1945, Hancock, (MEP Acc. 848), 2 ♂, 2 ♂ gen. (83/461, 83/462) [USNM]. UGANDA. *Karamoja District*: Loyoro (3°09'N, 34°12'E), 1955, A. J. Haddow, (SEAMP Acc. 111), 1 ♂ (1955/119), 1 ♂ gen. (79/242) [USNM]. SOUTH AFRICA. *Natal*: Zululand, Dukuduku Forest (28°23'S, 32°19'E), Apr. 1967, (SEAMP Acc. 297), 2 ♂ (M617 A, M516 A), 2 ♂ gen. (79/244, 85/203) [USNM].

Distribution (Fig. 7).—*Aedes cordellieri* is presently known from West Africa (Ivory Coast), East Africa (Kenya, Tanzania, Uganda) and South Africa. Other records of *taylori* from the Afrotropical Region will require confirmation owing to probable confusion with *Ae. cordellieri*.

Etymology.—This species is named to honor Dr. Roger Cordellier, Medical Entomologist, Services Scientifiques Centraux de l'O.R.S.T.O.M. (ORSTOM), and Chief, Medical Entomology Laboratory, ORSTOM-Institut Pasteur, Ivory Coast, in recognition and appreciation of his contributions to our knowledge of the mosquito fauna of Africa.

Taxonomic discussion.—Adults of *Ae. cordellieri* closely resemble those of *Ae. taylori* Edwards in the scutal markings but can be distinguished by the presence of yellowish scales on the apicolateral areas of terga II–VII. This same character state of *cordellieri*, however, is extremely similar to *Ae. furcifer* (Edwards), and when the scutal markings are rubbed off, *cordellieri* can easily be misidentified as *furcifer*. *Aedes cordellieri* can be distinguished from *furcifer* by the absence of pale scales on the dorsomedian areas of terga II–VII. In *furcifer*, there are scattered pale scales on the dorsomedian areas of terga II–VII. In *taylori*, there are no scattered pale, or yellowish scales on the abdominal tergites.

The male genitalia of *Ae. cordellieri* are very similar to those of *furcifer* and *taylori*. However, they can be distinguished easily from those of *furcifer*, as the gonocoxite lacks a projected lobe bearing numerous long setae on the apicomesal area. In this respect, *cordellieri* is the same as *taylori*. The male genitalia of *Ae. furcifer* have the gonocoxite with a distinct projecting lobe bearing numerous long setae on the apicomesal area. *Aedes cordellieri* is most closely related to *Ae. taylori*, with which it shares the following characters: gonocoxite short and broad, more or less truncate at apex, without a projecting lobe bearing numerous long setae on apicomesal area, with dense scales on mesal margin of ventral surface; claspette well developed; gonostylus elongate, slender, bifurcate just beyond middle, upper arm longer than the lower one, with a blunt, stout claw process apically on the shorter one. However, the male genitalia of *cordellieri* differ from those of *taylori* by the claspette, which has long apical part, with a row of scales along the mesal margin from apex to basomesal corner and with a row of short setae along the row of scales, followed by a few long, curved setae along the mesal margin of basal part, and without distinct, stout, long, pointed spines on median area of slightly expanded basal part (Fig. 3A). The male genitalia of *taylori* have a claspette



Aedes (Diceromyia) taylori Edwards

Fig. 6. *Aedes (Diceromyia) taylori*. Tergal aspect of the male genitalia.

with apical part short, narrow towards apex, broadened basally, with 4–5 small, short, pointed spines on mesal margin of apical part, with 2 rows of small, stout, short, pointed spines on basomesal corner, followed by 5–6 distinct, stout, long, pointed spines along the mesal margin of basal part, and with 3 (3–4) distinct, stout, long, pointed spines on median area of expanded basal part (Fig. 3B).

Bionomics.—In the Ivory Coast, the eggs of *Ae. cordellieri* were obtained from a female, biting man, at the ORSTOM study tower, 20 m above ground level, between 1730–1930 h, in Dezidougou; these were subsequently hatched and the larvae individually reared at SAMP. In Kenya, the immature stages of *Ae. cordellieri* have been collected in tree holes, in Gede, Coast Region and in Kerio Valley, Rift Valley Region.

The females of *Ae. cordellieri* were taken biting/landing on man, along with the

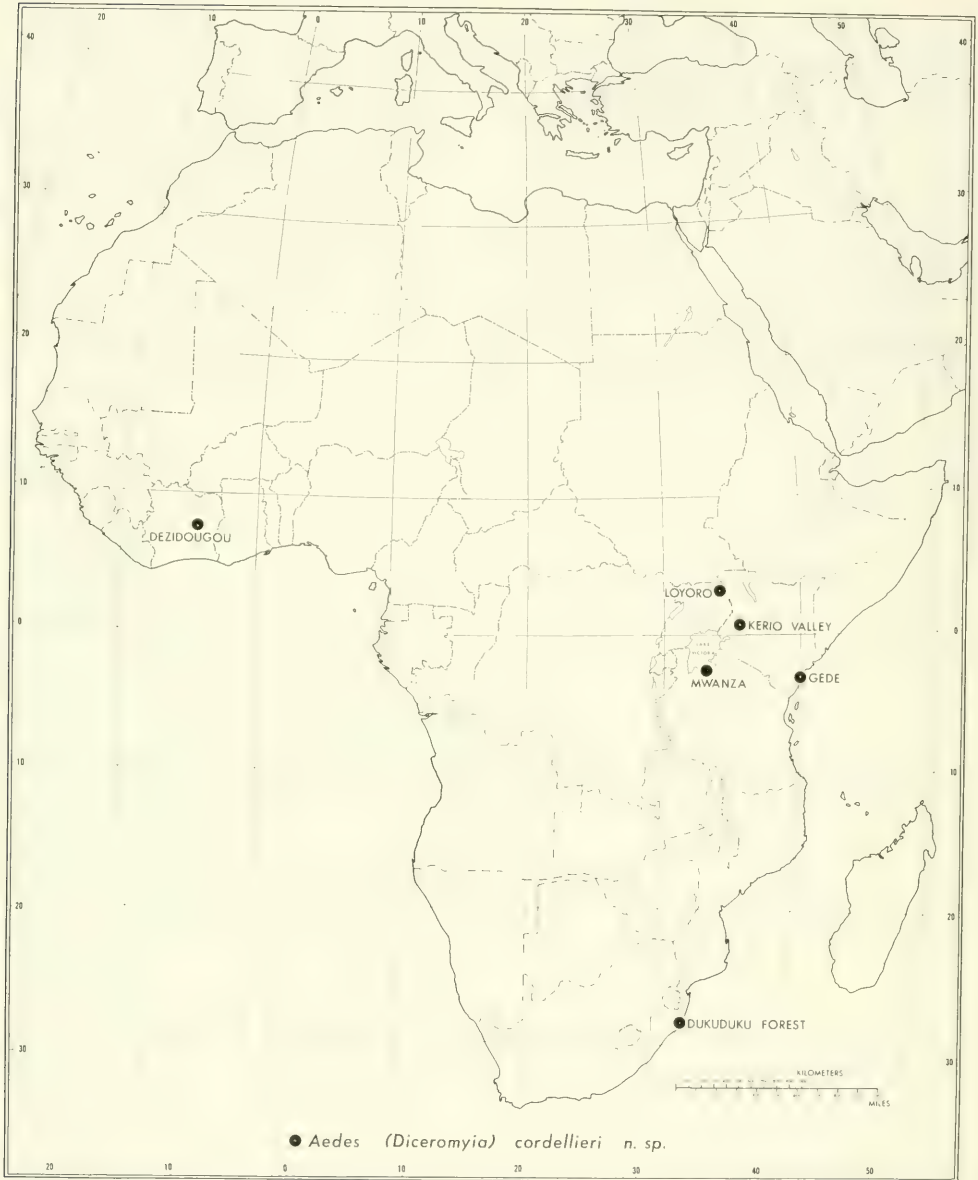


Fig. 7. Distribution of *Aedes (Diceromyia) cordellieri* in Africa.

females of *Ae. fuscifer*, at platforms (Dezidougou and Km 2 towers), 20 m and 12 m above ground level, in the evening, in the forest, M'Bahiakro, Centre Département, Ivory Coast.

Medical importance.—Lewis et al. (1942: 37) reported that *Ae. taylori* from Sudan [Anglo-Egyptian Sudan] is capable of transmitting yellow fever virus through biting under laboratory conditions. As *Ae. taylori* is a complex of 2 species, it is impossible to say which species were used in these experiments without examination of the aforementioned specimens. However, the present findings indicate

that the species previously called "*taylori*" in the eastern Africa (Uganda, Kenya and Tanzania) and South Africa (Natal) is *Ae. cordellieri*. The Sudanese material requires confirmation.

Aedes (Diceromyia) taylori Edwards

Figs. 3B, 6

Aedes (Diceromyia) taylori Edwards 1936: 55 (♂) or (♂, ♀).

Aedes (Diceromyia) taylori Edwards 1941: 216 (♂*, ♀; lectotype designation).

The description below is based on a topotypical specimen from Gadau, Nigeria, in the USNM [male, with 1 printed label data as "Pres. by/Imp. Inst. Ent./Brit. Mus./1931-500" and 1 hand printed label data as "N. P. Nigeria/gadau/ VIII-X-1931/A. W. Taylor," with associated genitalia on slide (83/458)] and the newly collected specimens from Dabakala, Ivory Coast.

Male.—*Genitalia* (Figs. 3B, 6): Gonocoxite short and broad, about 1.7 as long as wide (width measured 0.5 from base), less truncate at apex, without a projecting lobe bearing numerous long setae on apicomesal area, scales restricted to dorsolateral, lateral and ventral surfaces, with dense scales on mesal margin of ventral surface, with setae scattered on dorsomesal surface, mesal surface membranous; claspette long and broad, narrow towards apex, broadened basally, with 4–5 small, short, pointed spines on mesal margin of apical part, with 2 rows of small, stout, short, pointed spines on basomesal corner, followed by 5–6 distinct, stout, long, pointed spines along the mesal margin of basal part, and with 3 (3–4) distinct, stout, long, pointed spines on median area of expanded basal part; gonostylus elongate, slender, about 0.67 length of gonocoxite, bifurcate at about 0.55 from base, upper arm longer than the lower one, with a blunt, stout claw process apically on the shorter one; aedeagus with strongly toothed lateral plates; paraproct without apical teeth, cercal setae absent; apical margin of tergum IX slightly concave medially with 4 (2–6) setae on each side; sternum IX with 5–8 setae.

Material examined.—42 specimens: 28 adults (18 ♂, 10 ♀), 10 ♂ genitalia, 4 ♀ genitalia from Ivory Coast, Nigeria and Senegal.

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A NEW *PACHODYNERUS* FROM MAYAGUANA ISLAND, BAHAMAS,
AND A KEY TO THE WEST INDIAN SPECIES OF THE GENUS
(HYMENOPTERA: VESPIDAE: EUMENINAE)

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Abstract. — *Pachodynerus linda* n. sp. is described from Mayaguana I., Bahamas. Taxonomic, comparative and distributional notes, as well as a key, are provided for the 10 West Indian species of the genus. Lectotypes are designated for *Vespa atrata* Fabricius, *Vespa cinerascens* Fabricius, *Odynerus sanctivincenti* Ashmead, *Odynerus grenadensis* Ashmead, and *Odynerus cubensis* Saussure. *Pachodynerus scrupeus* var. *bahamensis* Bequaert and Salt, is recognized as a subspecies of *cubensis* Saussure (new status). The generic name *Monobiella* Ashmead, is synonymized under *Pachodynerus* Saussure, 1875 (new synonymy).

In 1983 I had the opportunity to visit briefly Mayaguana, one of the southernmost islands in the Bahamas. It is located midway between Acklins I. and the Caicos Is. Mayaguana is about 26 miles long and 7 miles wide. Its maximum elevation is 110 feet, and the island is xeric and sandy. The area that I explored, the coast of Abraham Bay near Start Point, was covered by mixed scrubby vegetation including small trees and scattered palms. I collected in late afternoon from about 3 to 6 PM. The only wasp taken proved to be an undescribed species of *Pachodynerus*. The species is described now so that a name will be available to others currently working on the genus.

It is not my intention here to provide a comprehensive treatment of the West Indian species of *Pachodynerus*, but before describing the new species I had to familiarize myself with the Caribbean members of the genus, and it seems appropriate to record what I have learned. Bequaert (1948), in his review and key to the West Indian *Pachodynerus*, treated only seven species, but there are at least ten, including the new one. Therefore, I have provided a key to species and descriptive and taxonomic notes for each of them. Although I have examined material from Trinidad, I have not made an effort to elucidate all the species that may occur on this continental island. I have relied on Bequaert's (1948) and Zavattari's (1912) interpretations of most Caribbean names in *Pachodynerus*, but I did borrow type material of many of the oldest species, especially those not studied by these authors.

The insect fauna of the West Indies is still poorly known except for the larger islands and a few of the small islands commonly visited by vacationers. Many islands remain unsampled or inadequately sampled, at least for *Pachodynerus* and other wasps, and additional endemics such as the one described here may be

found on them. In particular, islands in the Caicos group and some of the southern islands in the Bahamas such as Acklins, Crooked, and Great Inagua, need to be surveyed. Other Bahamas islands that seem to have been ignored by collectors are Andros, Grand Bahama, Great Abaco and Great Exuma.

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***Pachodynerus linda* Menke, NEW SPECIES**

Fig. 1

Description of female.—*Color*: Dull black except front face of pronotum, legs, and sternum II shiny; face including scape weakly shining; frons with yellow spot between antennal socket and eye margin; wings uniformly amber. *Vestiture*: Body generally covered by erect white setae whose length ranges from slightly less than to slightly more than 1 midocellus diameter; setae of terga I–II sparse, slightly decumbent. *Structure*: Margin of clypeal lobe slightly concave; clypeal surface shallowly punctate, punctures somewhat elongate vertically, not sharply defined, accompanied by feeble vertical rugae, punctures smaller, evanescent toward eye; frons densely, coarsely punctate, punctures deep, sharply rimmed, nearly contiguous but of irregular shape, a small impunctate area in front of midocellus and on outside of hindocellus, interocellar area flat; thorax slightly longer than wide (ratio: 44:40 or 43:38; length measured along midline from pronotal carina to hindmargin of metanotum; width measured across tegulae); pronotal dorsum densely, deeply, irregularly punctate, punctures subcontiguous, somewhat larger and deeper than those on scutum; scutum densely, deeply, somewhat irregularly punctate, punctures contiguous; scutellar punctation similar to pronotal dorsum; metanotum without obvious transverse crest, but when viewed in profile from in front, several teeth are visible between coarse, shallow, contiguous punctation; mesopleuron (except preomaulal area and area between midcoxa and scrobe) coarsely, closely irregularly punctate, punctures subcontiguous, flat bottomed, some large enough to be termed foveae; metapleuron smooth, dull, except for few weak ridges and punctures dorsad; propodeum with rounded posterolateral process that is directed posterad (Fig. 1), and a weak, interrupted carina between it



Fig. 1. Rear half of thorax and base of gaster of *Pachodynerus linda*.

and metanotum; dorsolateral area of propodeum foveolate, foveolation extending onto tooth and onto upper part of propodeal side as punctures; propodeal hindface dull, impunctate, with crescentic carinae near petiole socket, median carina of hindface dull; tergum I without transverse carina at crest of anterior vertical face, dorsum sparsely, very shallowly punctate, punctures 2 to 4 diameters apart, but becoming denser, deeper toward hind and lateral margins; punctures of II sparse, very shallow, almost imperceptible on disk, but becoming deeper, denser (1–2 diameters apart) laterally and apically; sternum II with rounded, transverse swelling near base, disk broadly shallowly concave, shiny, punctate, punctures somewhat open behind, 1 to 3 diameters apart. *Length*: 10.5–11 mm.

Male.—Unknown.

Types.—Holotype ♀ and four ♀ paratypes: Abraham Bay, Mayaguana I., Bahamas, April 24, 1983, A. S. Menke. Holotype and three paratypes deposited in the National Museum of Natural History. One paratype deposited in the Museum of Comparative Zoology, Harvard University, Cambridge.

Etymology.—*P. linda*, a noun in apposition, is affectionately dedicated to Linda Ann Hollenberg, collecting companion and dear but elusive friend. The name has the same stem as the Spanish word *lindo* that means pretty which accurately describes both the wasp and Ms. Hollenberg.

Discussion.—The black body and amber wings of *linda* easily set the species

apart from all other West Indian *Pachodynerus*. Morphologically the species is probably closest to *cinerascens*, but the latter has a transverse carina on tergum I, and the punctation of I–II is close with the interspaces roughened. The wings of *cinerascens* are violaceous. Possibly *P. linda* is endemic to Mayaguana although I have seen no *Pachodynerus* from nearby Caicos or Acklins Is.

KEY TO WEST INDIAN *PACHODYNERUS*

1. Tergum I entirely black	2
– Tergum I with yellow apical band	5
2. Terga II–V or VI yellow banded apically; pronotum margined with yellow; metanotum yellow banded, upper propodeal lamella yellow, legs with yellow stripes; sternum II flat; ocellar triangle longitudinally channeled; (Cuba, Isle of Pines, Grand Cayman, Jamaica, Hispaniola, Puerto Rico, St. Thomas, New Providence I., San Salvador I., Dominica, Trinidad)	<i>nasidens</i> (Latreille)
– Thorax, legs and gaster without yellow; sternum II transversely depressed near base (concave in lateral profile); ocellar triangle flat	3
3. Tergum I without transverse carina at top of basal declivity; tergum II dull, sparsely, weakly punctate except along hindmargin; wing veins and membrane amber (Mayaguana I.)	<i>linda</i> Menke, n. sp.
– Tergum I with transverse carina; tergum II moderately to strongly shining, covered with obvious punctation; wing veins dark brown or black, membrane smoky or violaceous at least along front margin	4
4. Posterolateral process of propodeum sharp apically, thornlike; scutum and scutellum smooth, shiny, with shallow punctures separated by 1–2 diameters; tergum II smooth, shiny, sparsely, shallowly punctate; male clypeus yellow at least in middle (Puerto Rico, Vieques I., St. Thomas, St. John, Guana I., Virgin Gorda, St. Martin, Anegada, Saba, St. Eustatius, St. Kitts, Barbuda, Montserrat)	<i>atratus</i> (Fabricius)
– Propodeal process bluntly rounded apically; scutum and scutellum deeply, coarsely, nearly contiguously punctate, interspaces weakly shining; tergum II dull, densely, shallowly punctatorugose; male clypeus black (St. Croix, St. Thomas)	<i>cinerascens</i> (Fabricius)
5. Legs black with yellow maculations	6
– Legs reddish brown and yellow, or largely reddish brown (coxae sometimes black)	9
6. Pronotal dorsum margined by yellow anteriorly and posteriorly, or completely yellow and gena all black; propodeal lamella not forming a posterolateral angle or toothlike process; a downward projecting fingerlike process (often yellowish) associated with mesopleural scrobe (Antigua, Montserrat, Guadeloupe, Dominica, Martinique, St. Lucia, Barbados, St. Vincent, Canouan I., Grenada)	<i>guadulpensis</i> (Saussure)
– Pronotum yellow margined only anteriorly*; gena sometimes with yellow spot; propodeal lamella forming a posterolateral toothlike process or angle; mesopleuron merely angular adjacent to scrobe, without long process	7

* If narrowly margined by yellow posteriorly (Great Inagua I.) then gena has yellow spot.

7. Inner margins of ocelli surmounted by swellings, hindocelli sunken, inter-ocellar area usually longitudinally channel-like; gena with yellow spot (Cuba) *alayi* Bequaert
- Inner margins of ocelli not surmounted by integument, ocelli not sunken, interocellar area flat; gena all black or with yellow spot (Hispaniola, Mona I., Great Inagua I.) *tibialis* (Saussure) 8
8. Gena and female ocular sinus all black; yellow bands on terga I–II and sternum II essentially uniform in width (Hispaniola, Mona I.) .. *tibialis* s. s.
- Gena with elongate yellow spot; female ocular sinus partly yellow; yellow bands on terga I–II and sternum II abruptly expanded laterally to at least twice width of band at midline (Great Inagua I.) *tibialis* subsp. *barbouri* Bequaert
9. Tergum I with coarse punctures in black area; propodeal hindface covered with coarse, crescentic ridges (Jamaica) *jamaicensis* Bequaert and Salt
- Tergum I impunctate in black area or at most with sparse, shallow punctures; propodeal hindface at most with few, fine crescentic ridges near petiole socket, unridged dorsad (Cuba, Cayman Is., Bahamas) 10
10. Tergum I with very shallow, sparse punctures basad of yellow band at least laterally; gena largely yellow or with elongate yellow spot; tergum I black* with yellow band (Cuba, Bahamas) *scrupeus* (Zavattari)
- Tergum I impunctate basad of yellow band; gena completely black or if with small yellow spot (Bahamas) then tergum I tricolored (largely reddish brown except for apical yellow band with narrow black zone preceding it) (Cuba, Cayman Is., Bahamas) *cubensis* (Saussure) 11
11. Tergum I tricolored (reddish brown, black and yellow), terga III–VI or VII black (Bahamas) *cubensis* subsp. *bahamensis* Bequaert and Salt
- Tergum I bicolored (black and yellow), tergum III apically, IV–VI or VII completely reddish brown (Cuba, Cayman Is.) 12
12. Scutellum with two large yellow spots; yellow bands of terga I–II similar in width (Cuba, Little Cayman I.) *cubensis* (Saussure) s.s.
- Scutellum black or with two tiny yellow spots (= to one or two ocellus diameters); tergum II without yellow band or at most with band that is much narrower than that on I (Grand Cayman I.) *cubensis* subsp. *caymanensis* Soika

Genus *Pachodynerus* Saussure

Among the 10 West Indian species of this genus that I recognize, three were not mentioned by Bequaert (1948) in his review of Caribbean *Pachodynerus*. They were *atratus* (Fabricius), *cinerascens* (Fabricius) and the new species, *linda*. The first two are unusual in that they have a transverse carina on tergum I, and Bequaert (1929) earlier assigned them to *Monobiella*, which he regarded as a subgenus of *Pachodynerus*. His omission of these two species in his 1948 paper may indicate that by that time he regarded *Monobiella* as a distinct genus.

Ashmead (1900) established *Monobiella* for *atratus*, and later (Ashmead, 1902) indicated that the species had five segmented maxillary palpi. However, as Za-

* Vertical slope of tergum I rarely reddish brown in some specimens from New Providence I., Bahamas.

vattari (1912) correctly stated, the palpi of *atratus* have the usual six segments. That leaves only the tergal carina as a possible generic character for *Monobiella*. Carpenter and Cumming (1985), in their fine discussion of character states in the Eumeninae, pointed out the variable nature of the tergal carina in the subfamily, and stated that it has been given too much weight as a generic character. I concur. The tergal carina of *cinerascens* is weaker than in *atratus*, and based on other morphology the two species are probably not closely related. In other species of *Pachodynerus* tergum I is somewhat angulate at the top of its vertical face (*jamaicensis*, *linda*, *tibialis*). Thus the tergal carina is suspect as a generic (or subgeneric) character and I am synonymizing *Monobiella* with *Pachodynerus* (NEW SYNONYMY).

Pachodynerus alayoi Bequaert

Pachodynerus alayoi Bequaert, 1948. Psyche 55:110. Holotype ♂, Siboney, Cuba (MCZ).

This wasp is apparently a Cuban endemic. The black legs with yellow on the femora, tibiae, and tarsi, separate *alayoi* from *cubensis* and *scrupeus*, two of the three other Cuban species. The legs are reddish with yellow markings in *cubensis* and *scrupeus*. The gena has an elongate yellow maculation as in *scrupeus*. The yellow band on tergum I separates *alayoi* from *nasidens*, the remaining species known to occur in Cuba. Tergum I is entirely black in *nasidens*.

Bequaert (1948) stressed that the upper propodeal lamella (or carina) is "poorly developed, low, and irregular, not forming a complete lamella," but in the female and two males available to me, it is continuous from the posterolateral angle nearly to the metanotum. In one male and the female, the carina is low, its crest undulating, similar in this respect to some Bahamian specimens of *scrupeus*. Overall the lamella is not as high as in most species of *Pachodynerus*, and Jim Carpenter (in litt.), after examining Bequaert's type, says that it is very low, indistinguishable from the adjacent propodeal rugae. Obviously more material of *alayoi* is needed to determine the extent of variation in this species.

Pachodynerus atratus (Fabricius)

Vespa atrata Fabricius, 1798. Suppl. Entomol. Syst., p. 262. Five syntypes, ♂, ♀, "Americae meridionalis insulis" Dom. Lund [type locality here restricted to St. Thomas] (Mus. Copenhagen). One male selected and labeled as lectotype (present designation).

Rhynchium atratum, Dewitz, 1881. Berl. Entomol. Z. 25: 200. Listed from Puerto Rico.

Monobiella atrata, Ashmead, 1900. Trans. Entomol. Soc. Lond. 1900: 312. Listed from Puerto Rico.

Odynerus atratus, Zavattari, 1912. Arch. Nat. 78A: 192. Redescribed, listed from Puerto Rico and St. Thomas.

Vespa atrata, Schulz, 1912. Berl. Entomol. Z. 57: 82. Notes on types, cites St. Thomas as a locality.

Monobiella atrata, Wolcott, 1924. J. Dept. Agric. Porto Rico 7: 41. Listed from Puerto Rico.

Pachodynerus atratus, Bequaert, 1929. Ann. Entomol. Soc. Am. 22: 558. First assignment to *Pachodynerus*.

- Monobiella atrata*, Wolcott, 1936. J. Agric. Univ. Puerto Rico 20: 568. Listed from Puerto Rico.
- Pachodynerus* (sic) *atratus*, Wolcott, 1941. J. Agric. Univ. Puerto Rico 25: 156. Listed from Puerto Rico.
- Pachodynerus atratus*, Wolcott, 1951. J. Agric. Univ. Puerto Rico 32: 861. Listed from Puerto Rico.
- Pachodynerus atratus*, Simonthomas, 1984. Stud. Fauna Curacao Caribbean Is. 67: 94. Recorded from St. Martin, Saba, Montserrat, and St. Kitts.

This is a distinctive species. The body is entirely black (except for the yellow male clypeus and stripe sometimes on the scape), and the integument is shiny. Unlike most *Pachodynerus*, *atratus* is rather sparsely, shallowly punctate. The propodeum has a downward projecting, thornlike posterolateral process (reduced in occasional specimens), and usually there is no carina or lamella between it and the metanotum (occasional specimens have a partial carina). In one of Fabricius' syntypes, as well as the two males from Barbuda that I have seen, the propodeal process is merely angulate or rounded off. Among West Indian species of the genus, the absence of the propodeal carina or lamella is shared only with *cinerascens*, although some specimens of that species have a weak carina. The strong transverse carina on tergum I is also distinctive, although *cinerascens* has a weak one. The hypoepimeron projects ventrad over the scrobe as an acute point in *atratus*, but not in *cinerascens*. Although *atratus* has some features that isolate it from other species of *Pachodynerus*, none warrant placing it in a separate genus or subgenus in my opinion.

Schulz (1912) studied Fabricius' syntypes and my examination of them confirms that his interpretation of *atratus* was correct. The Sehestedt and Tonder Lund Collection in Copenhagen contains two males. The one in the best condition bears a handwritten label "V. atrata ♂" that Ole Lomholdt says was from the pen of either Sehestedt or Lund. Three additional specimens, one male and two females, are present in the Kiel University Collection now housed in Copenhagen. One female has a handwritten label "atrata" whose reverse side reads "V. ex Ins. S. Thomae." Since Fabricius specifically mentions "Dom. Lund" in the original description, I am selecting one of the S. and T. Lund males as lectotype, and have so labeled it. It is the male without the handwritten label. J. van der Vecht placed a lectotype label on this specimen in 1963, but never published it. Although it is missing all but tergum I of the gaster and the antennae past flagellomere I, the propodeal processes are well formed and typical for the species. The other male, although much more intact, has poorly formed propodeal processes, and for that reason I have decided not to use it for the lectotype. Based on the locality data associated with the female in the Kiel Collection I hereby restrict the type locality of *atratus* to St. Thomas.

Pachodynerus atratus occurs from Puerto Rico to Montserrat in the northern Leeward Islands. The clypeus is entirely yellow in males from Barbuda, but those from Puerto Rico, St. Thomas and Montserrat only have a yellow zone down the middle third of the clypeus. The clypeus of Fabricius' males is similarly colored. The male scape varies from all black to black with a yellow stripe on its outer (lower) face. The stripe is best developed on material from Barbuda. Miskimen and Bond (1970) list *atratus* from St. Croix, but I cannot confirm this and suspect a misidentification. There are two females of *atratus* in the Museum of Compar-

ative Zoology labeled Barbados, but this is far from the rest of the species' range and an error in labeling is probable.

***Pachodynerus cinerascens* (Fabricius)**

Vespa cinerascens Fabricius, 1775. Syst. Entomol., p. 369. Two syntypes, ♀, "America" v. Rohr. [type locality here restricted to St. Croix] (Mus. Copenhagen). Lectotype hereby designated.

Odynerus cinerascens, Zavattari, 1912. Arhiv Naturges. 78A: 221. Redescribes species based on material in Berlin Museum labelled "America."

Rhynchium cinerascens, Schulz, 1912. Berl. Entomol. Z. 57: 82. Studied Fabricius' types.

Pachodynerus cinerascens, Bequaert, 1929. Ann. Entomol. Soc. Am. 22: 558. First assignment to *Pachodynerus*.

Pachodyneurus (sic) *cinerascens*, Beatty, 1944. J. Agric. Univ. Puerto Rico 28: 171. First clear record from St. Croix. Nesting in limestone cliffs.

Pachodynerus cinerascens, Miskimen and Bond, 1970. N. Y. Acad. Sci., Sci. Surv. Porto Rico Virgin Is. 13: 110. Recorded from St. Croix.

Being wholly black with violaceous wings, this wasp is unlikely to be confused with any other West Indian *Pachodynerus* except *atratus*. The key characters make identification straightforward.

Two syntypes are housed in the Kiel University Collection now housed in Copenhagen. One bears Fabricius' handwritten label "cinerascens." J. van der Vecht placed a lectotype label on this female in Aug. 1959, but never published it. This is the specimen that I have chosen as lectotype, and it is so labeled. The tergal carina is weak in both specimens, but otherwise they agree with other material available to me.

Fabricius' material was collected by von Rohr. According to Zimsen (1964), von Rohr collected insects in the West Indies, and established a botanic garden in St. Croix in the Virgin Islands. Nearly all material seen by me is from St. Croix, and I hereby restrict the type locality to that island. The species also occurs on St. Thomas (Montana State University).

***Pachodynerus cubensis* (Saussure)**

Odynerus cubensis Saussure, [1853]. Etudes sur la Famille des Vespides. 1: 181, pl. 18, fig. 8. Syntypes, ♂, ♀, Cuba (Mus. Paris, Mus. Genoa). Lectotype ♀, "Cuba", present designation (Mus. Paris).

Pachodynerus scrupeus var. *bahamensis* Bequaert and Salt, 1931. Ann. Entomol. Soc. Am. 24: 786. Holotype ♀, Mangrove Cay, Andros I., Bahamas (Museum of Comparative Zoology). NEW STATUS.

Pachodynerus scrupeus var. *bahamensis*, Bequaert, 1948. Psyche 55: 112. Description of male, distribution.

Pachodynerus scrupeus var. *bahamensis*, Krombein, 1953. Am. Mus. Novit. (1633): 8. Distribution.

Pachodynerus cubensis ssp. *caymanensis* Soika, 1969. Mem. Soc. Entomol. Ital. 48: 384. Holotype ♀, Rum Point, Grand Cayman (BMNH).

Pachodynerus scrupeus var. *bahamensis*, Elliott et al., 1979. Proc. Entomol. Soc. Wash. 81: 355. Synonymizes *bahamensis* with *scrupeus*.

I have examined two female syntypes of *cubensis* from the Paris Museum and confirm that Zavattari's (1912) interpretation of this species, which was based on Saussure's color figure on plate 18, was correct. One specimen bears a handwritten label "Cuba," and also a lectotype label placed on it by R. M. Bohart in 1960. The latter has never been established in print. I have selected this specimen as lectotype and placed a label on it.

Pachodynerus cubensis is very similar to *scrupeus*, the other red and yellow legged *Pachodynerus* found in Cuba. However, the tergal differences in the key seem to separate them consistently. In Cuba seemingly reliable color differences separate the two species also, but in the Bahamas where they occur sympatrically, the color patterns are less diagnostic. Typical *cubensis* has a completely black gena, the scutellum has two large but discrete yellow spots, and tergum I has a narrow, parallel sided yellow band whose width is not more than one third the dorsal midlength of the plate. This band usually expands abruptly as it turns downward laterally. Sternum I is usually reddish brown or black (yellow in one female seen). The female clypeus usually has a linear black spot near its apex and is narrowly black laterally along the margin. The ocular sinus of the frons is nearly always completely black in females from Cuba (one out of five specimens from Havana in USNM has yellow in the sinus). Males of *cubensis* agree with both sexes of *scrupeus* in apparently always having a yellow macula in the ocular sinus. Gastral segments III-VI or VII are reddish brown (only apically on III) in *cubensis*. The hindfemur is largely brownish or blackish in occasional females from Cuba.

In Cuba *P. scrupeus* has as elongate yellow macula on the gena (the gena is often largely yellow), the scutellum has a single transverse yellow spot, tergum I has a broader, more irregular yellow band, and sternum I is yellow. The female clypeus lacks the linear mesal black spot in the few specimens available to me. Although *scrupeus* usually has a reddish brown gastral tip, segment III is usually black and occasional specimens have the remaining terga dark also.

There seem to be few morphological differences between *cubensis* and *scrupeus*, and none are particularly striking. In *cubensis* the black horizontal part of tergum I is impunctate, while in *scrupeus* large, shallow, sparse punctures are visible. Tergum I in *cubensis* is vaguely angular at the interface between the vertical and horizontal faces. In *scrupeus* this area is simply rounded. The upper propodeal lamella is uniformly high in *cubensis*, but it is sometimes low and irregular in *scrupeus*. Interestingly, the humeral carina, a generic character for *Pachodynerus*, is often weak in males of both species, and is evanescent in one specimen of *P. cubensis bahamensis*.

Pachodynerus cubensis is unrecorded from the Bahamas, but the taxon *bahamensis*, described by Bequaert and Salt (1931) as a variety of *scrupeus*, appears to me to be more properly assignable to this species (NEW STATUS). This opinion is based on tergum I which is impunctate like that of *cubensis* and has the same vague angulation at the crest. The propodeal lamella is distinct but lower than in Cuban material of *cubensis*. The color pattern tends to corroborate the transfer of *bahamensis* from *scrupeus* to *cubensis*, and subspecific rank seems justified based on the distinctive tricolored abdomen. Elliott et al. (1979) synonymized *bahamensis* under *scrupeus* based on material of both collected on San Salvador I. My examination of their material indicates that two species are present and that their synonymy was erroneous.

I have seen *bahamensis* from the following islands: South Bimini, New Providence, Eleuthera, San Salvador, Rum Cay, and Long Island. Bequaert's type is from Andros. Color in *P. cubensis bahamensis* differs from Cuban specimens in the following ways: tergum I is almost entirely reddish brown except for the apical yellow band and a narrow black area immediately in front of it, and III–VI or VII are all black. In a female (FDA) from Eleuthera (Rainbow Bay) most of the vertical slope of tergum I is black. The usual reddish brown color is reduced to a zone at the crest with downward extensions laterally. Accompanying males are typically colored.

There is color pattern variation from island to island and even within an island population in *bahamensis*. The middle and lateral black areas of the female clypeus are united forming a W in one of two specimens from Long I., and in two of six specimens from San Salvador. The apical half of the clypeus is black in the single female seen from New Providence I., and in the two from South Bimini. The gena of the two Long I. females has a yellow spot that is smaller than an ocellus, and in the single Rum Cay female seen it is larger and elongate, but smaller than the similar maculations found in *scrupeus*. The female ocular sinus has a yellow spot in the Rum Cay specimen and in one of the Long I. specimens.

Pachodynerus cubensis also occurs in the Cayman Islands (Grand Cayman and Little Cayman—USNM). The female color pattern on material from Grand Cayman, the farthest island from Cuba, is atypical: the lower one half to two thirds of the clypeus is black, the ocular sinus is partly yellow, the yellow spots on the scutellum are tiny, varying from one to two ocellus diameters in size, and tergum II lacks an apical yellow band or it is very narrow. Females from Little Cayman have the typical narrow black spot on the lower middle of the clypeus, the ocular sinus is black, the scutellum has the typical large yellow spots, and tergum II has a broad yellow band. Males from Grand Cayman vary. Five of the seven specimens available have a broad yellow band on tergum II as in typical *cubensis*, the other two have a very narrow one. The yellow scutellar spots are very tiny as in the female, or are absent. No males are available from Little Cayman. Soika (1969) described the Grand Cayman population as a subspecies, *caymensis*, and recognition of this taxon seems justified.

Pachodynerus gadulpensis (Saussure)

Odynerus gadulpensis Saussure, [1853]. Études sur la Famille des Vespides. 1: 182. Type ♀, "La Guadeloupe" (Mus. Paris).

Odynerus sanctivinceni Ashmead, 1900. Trans. Entomol. Soc. Lond. 1900: 233. Lectotype ♀, Kingstown, St. Vincent (USNM), present designation.

Odynerus grenadensis Ashmead, 1900. Trans. Entomol. Soc. Lond. 1900: 234. Lectotype ♀, St. Georges, Grenada (USNM), present designation.

Odynerus guadelupensis Dalla Torre, 1904. Genera Insectorum, Fasc. 19, Vespidae, p. 46, lapsus or emendation.

Pachodynerus gadulpensis sanctivinceni Willink, 1972. Proc. Kon. Nederl. Akad. Wet. (C)75: 71. Lapsus.

Pachodynerus gadulpensis occurs from Antigua and Montserrat to Grenada in the Lesser Antilles, and is recorded from many of the intervening islands. The

yellow margins of the pronotal dorsum combined with the yellow apical band on tergum I immediately identify the species.

There is considerable interisland color variation in *guadulpensis* and not all of it is clinal. The pronotal dorsum is entirely yellow in material from Guadeloupe, Martinique, St. Lucia, St. Vincent and Canouan I. It is nearly all yellow in specimens from Barbados and Grenada (I have not seen material from Antigua and Montserrat), but in material from Dominica there is a large black zone laterally. Only terga I–II have yellow bands in material from Guadeloupe, Dominica and Grenada. Tergum III has a narrow yellow band in females from Martinique, St. Lucia and Canouan I. (males from Martinique have narrow bands on III–IV). All terga are banded in material from St. Vincent, and tergum II often has a lateral yellow spot in females. The sterna also vary in the amount of yellow banding but it is mainly in the degree of band width. Generally all sterna, except I, have bands except in specimens from Dominica. On this island some males only have a yellow band on sternum II, or on II–III. Southward there is a reduction in the amount of black on the female clypeus. It is all yellow in the single specimen from Canouan I., and in all females from St. Vincent. However, the female clypeus has a large black zone in material from Grenada, an island south of St. Vincent.

Bequaert (1948) treated the St. Vincent population as the "variety" *sanctivincenti* (Ashmead) because of its extensive yellow maculations (scutellar spots very large, nearly fused; yellow band of tergum I enlarged laterally, tergum II sometimes with yellow spots, terga III–VI yellow banded, female clypeus entirely yellow, etc.). Willink (1972) apparently regarded *sanctivincenti* as a subspecies, but in view of the variety of island color forms in *guadulpensis* I feel that such recognition is premature. Long series of specimens from all of the islands within the range of *guadulpensis* should be analyzed before making a decision on subspecies recognition.

Bequaert (1948) and Willink (1972) synonymized *grenadensis* (Ashmead) with *guadulpensis* and I concur. Types of this name, as well as *sanctivincenti*, are housed in the British Museum (Natural History) and the National Museum of Natural History (USNM). I have selected lectotypes for these two names from the USNM material.

The USNM Collection contains a series of wasps from Trinidad that are similar structurally to *guadulpensis*, but their color pattern and setation are different. Presumably the material Callan (1954) mentioned from Trinidad under the name "*Odynerus* sp. near *grenadensis* Ashmead" is the same. All of the terga (except VI in the female) and sterna (except I) are yellow banded or maculated similar to *guadulpensis* from St. Vincent, but the pronotal dorsum is black laterally, the scutellum only has two small yellow spots, and the female clypeus is largely black. The head and thoracic dorsum are fairly densely covered by golden, decumbent setae, as well as erect setae of the same color. The facial and thoracic hair of *guadulpensis* is generally darker and consists mostly of erect and somewhat sparser setae. Like *guadulpensis*, the Trinidad specimens have a yellowish projection over the scrobe, and the upper propodeal lamella does not form a posterolateral tooth or angle. These morphological features are also found in the South and Middle American species *praecox* (Saussure), the name that apparently should be used for the Trinidad species. However, typical *praecox* has yellow bands only on terga I–II, but in northern South America the species has the same extensive yellow banding found in the Trinidad specimens, and the same decumbent golden pu-

bescence. The name *zonatus* (Saussure), which Willink (1972) synonymized under *praecox*, applies to these extensively yellow banded specimens. Saussure (1875) suggested that his *zonatus* might be a "variety" of *guadulpensis*.

Further study may indicate that *praecox* is conspecific with *guadulpensis* as Zavattari (1912) suggested. The latter name has priority. However, there is one morphological feature in the males of the Trinidad material that casts doubt on this. Unlike *guadulpensis*, the apex of tergum I is depressed coinciding with the yellow band, and the punctures there tend to be very deep, contiguous, and their edges spiculate, at least in the middle of the plate. This condition also occurs in mainland *praecox* from Venezuela. In males of *guadulpensis*, the apex of tergum I is slightly depressed, but the punctuation there is not abnormal.

Pachodynerus jamaicensis Bequaert and Salt

Pachodynerus jamaicensis Bequaert and Salt, 1931. Ann. Entomol. Soc. Am. 24: 787. Holotype ♂, Montego Bay, Jamaica (American Museum of Natural History).

The coarsely ridged propodeal hindface, the coarse punctures of tergum I, and the suggestion of a transverse ridge at the base of tergum I make *jamaicensis* one of the more distinctive West Indian species. The reddish brown legs and yellow bands on terga I-II are supplementary recognition features. The species is apparently endemic to Jamaica.

Pachodynerus nasidens (Latreille)

Odynerus nasidens Latreille, [1817]. Insectes de l'Amerique Equinoxiale . . . Humboldt et Bonpland, vol. 2, livr. 10, p. 112. ♀, origin unspecified (Museum Paris?).

Odynerus simplicicornis Saussure, [1855]. Études sur la Famille des Vespides, vol. 3, p. 253. ♂, Cuba (Mus. Paris). Synonymy by Zavattari, 1912; Bequaert, 1948; Willink, 1972.

Odynerus auratus Saussure, 1858. Rev. Mag. Zool. (2)10: 166. ♀, "Mexique." Type depository unknown. Synonymy by Saussure, 1875, Zavattari, 1912.

Odynerus nasidens var. *minor* Saussure, 1875. Smithson. Misc. Coll. 254: 233. Syntypes, ♂, ♀, Mexico (?). (Mus. Geneva ?). Synonymy by Bohart, 1951.

Odynerus magdalenae Kriechbaumer, 1900. Berl. Entomol. Z. 45: 105. Type ♀, "Columbien: Puerto Berrio am R. Magdalena" (Mus. Munich).

Odynerus magdalenae, Schulz, 1903. Berl. Entomol. Z. 48: 260. Synonymy with *nasidens*.

Odynerus clavilinus Cameron, 1912. Timehri, J. R. Agric. Soc. Brit. Guiana (3)2: 222. Syntypes, ♂, ♀, British Guiana (BMNH).

Odynerus clavilinus, Soika, 1941. Boll. Soc. Veneziana Stor. Nat. 2: 248. Synonymy with *nasidens* (♀ only); also misspelled *clavilineatus* on same page.

Odynerus clavilineatus (sic), Willink, 1972. Proc. Kon. Nederl. Akad. Wet. (C)75: 69. Synonymy with *nasidens* (♀ only).

This is the only yellow banded species in the West Indies with a completely black tergum I. Actually, a suffused band can often be seen laterally on tergum I under a microscope, but the plate appears black to the naked eye.

P. nasidens is widespread in the Neotropical Region and it is known from the Greater Antilles, some of the Bahamas, and also Trinidad. It seems to be replaced in the Lesser Antilles by *guadulpensis*. *P. nasidens* occurs as far north as Arizona,

Texas and southern Florida and may have been introduced to the last state. It has been introduced (records from specimens in USNM) to the Hawaiian Islands, the Marquesas, Christmas I., Canton I., Eniwetok Atoll, Kwajalein Atoll, and Guam.

Pachodynerus scrupeus (Zavattari)

Odynerus scrupeus Zavattari, 1912. Archiv Naturges. 78A: 220. Syntypes, ♂, ♀, Cuba (Mus. Turin, Mus. Berlin).

When Zavattari (1912) described *scrupeus* he stated that it was very similar to *cubensis*, but that there seemed to be constant color differences between them. My study of the two species confirms this, but some slight morphological differences can be added. In *scrupeus* tergum I has sparse, shallow (faint) punctuation in the black area of the plate, and the interface between the vertical and horizontal parts is rounded. In *cubensis* tergum I is impunctate basad of the yellow band and is vaguely angled at the crest. Unfortunately, *scrupeus* is infrequently collected in comparison with *cubensis*, at least in Cuba, so that the diagnostic reliability of these tergal features must be regarded as provisional.

In Cuba the color pattern of *scrupeus* is as follows: the gena is largely yellow, or at least has an elongate spot; the ocular sinus of the frons is yellow; the female clypeus is entirely yellow (always?); the scutellum has one large, rectangular yellow spot, this is obviously attributable to the fusion of the two square or triangular spots found in *cubensis*—thus when more material is available, some Cuban *scrupeus* may be found to have two discrete spots also. Tergum I has a broad irregular, yellow band whose width at the midline is at least equal to half the plate's length, and the inner margin of this band is undulating, its width expanding laterally. Sternum I is yellow. The gaster is usually reddish brown apically (segments IV–VI or VII) just as in *cubensis*, but unlike that species, segment III is usually entirely black. I have seen one male of *scrupeus* in which terga IV–VII are blackish (also noted by Bequaert, 1948).

Pachodynerus scrupeus is known from La Habana and Oriente Provinces in Cuba. It also occurs sympatrically with *cubensis* in the northern islands of the Bahamas. I have seen material from North and South Bimini, Gun Cay, Eleuthera, New Providence, Andros, Cat I., San Salvador, and Rum Cay. The propodeal lamella varies in the Bahamian material. In some specimens it is only a low carina and it often becomes evanescent toward the propodeal base.

The color pattern of the Bahamian populations varies on some of the islands and differs from Cuban *scrupeus*. Unlike Cuban material, the yellow band on tergum I is fairly uniform in width and is similar to the band on II. The thickness of the band on I is about a fourth to a third the median length of the dorsal part of the plate. Usually its inner border is not undulating or step-like, but the band broadens gradually laterad except in material from the Bimini group. The band of tergum I is narrowest in this last population. In one of three males seen from New Providence, the vertical slope of tergum I is reddish brown, but this color does not extend to the horizontal surface as in *P. cubensis bahamensis*. All Bahamian *scrupeus* have two discrete yellow scutellar spots. These are square or triangular as in *P. cubensis*. These spots are only about three ocellar diameters in size on some specimens from South Bimini. Sternum I varies from yellow to reddish brown or combinations of both. The female clypeus is entirely yellow

except in the Bimini group. Here there is a large irregular, central black spot, and the clypeal border near the apex is broadly lined by black. In one South Bimini female the median and lateral spots are fused. In one of two females seen from San Salvador (SUNY) there is a round, ocellar-size, median black spot on the clypeus. Gastral segments III–VII are black in Bahamian males except in one of three seen from New Providence. In this specimen tergum VII and sterna VI–VII are reddish brown. Bahamian females usually have the last segment or two reddish brown, but in a few only the last sternum is so colored.

The scutellar spots, the more or less regular yellow band on tergum I, and the largely black gastral apex could be used to defend naming the Bahamian *scrupus* as a new subspecies, but I feel that much more material is needed before such an analysis can be safely made.

Pachodynerus tibialis (Saussure)

Odynerus tibialis Saussure, [1853]. Études sur la Famille des Vespides, vol. 1, p. 183. Holotype ♀, “La Colombie, Caracas,” Coll. Romand [type locality here restricted to Hispaniola] (Mus. Geneva).

Odynerus tibialis, Saussure, 1875. Smithson. Misc. Coll. 254: 241. Suggests that Hispaniola (“St. Domingo”) is the true provenance rather than Venezuela.

Pachodynerus tibialis var. *barbouri* Bequaert, 1948. Psyche 55: 109. Holotype ♀, Great Inagua, Bahamas (MCZ).

Pachodynerus tibialis, Bequaert, 1949. Bol. Entomol. Venezolana 7: 128. Says species is strictly Antillean.

Pachodynerus tibialis is one of a number of West Indian members of the genus that have yellow bands only on terga I–II, and sternum II. However, the black and yellow legs of *tibialis* separate it from all but *alayi* and some *guadulpensis*. In *guadulpensis* the pronotal dorsum is yellow margined in front and behind, the upper propodeal lamella does not form a posterolateral tooth or angle, and a narrow process projects downward over the mesopleural scrobe. *P. tibialis* has yellow only anteriorly on the pronotum (except in subspecies *barbouri*, see below), the propodeal lamella forms an angle posterolaterally, and the mesopleuron is merely angular near the scrobe. In these last two features *tibialis* is similar to *alayi*, but the latter is more extensively maculated with yellow. In *tibialis* s.s. the scutellum is usually entirely black, the gena is all black, the female ocular sinus is all black, the femora are all black, and the tibiae are yellow only on their outer surface. In *alayi* the scutellum has two yellow spots, the gena has an elongate yellow spot, the female ocular sinus has a yellow spot, the front and midfemora have yellow zones and all tibiae are extensively yellow. Structural differences between *tibialis* and *alayi* are not striking. The interocellar area is flat in *tibialis* but is usually channel-like in *alayi*. The ocelli in the latter are sunken due to the raised integument around their inner margins. The propodeal lamella is evenly arcuate from the process to the propodeal base in *tibialis*, but it is straight for most of its length in *alayi*. Tergum I in *tibialis* is somewhat angulate transversely at the top of the anterior vertical face (as in *cubensis*), while in *alayi* the tergum is simply rounded. The angulate tergum of *tibialis* suggests a close relationship with *cubensis*. As in that species tergum I is impunctate.

I have studied Saussure's apparent holotype female; his description does not suggest that he had more than one specimen. It is labelled “Carac.” and someone

has added a red "holotypus" label. Saussure's type conforms to the usual interpretation of *tibialis*. I have also seen the male from Haiti that Saussure (1875) subsequently described. He indicated in this later paper that his original female was probably mislabeled and that the species was an inhabitant of Hispaniola, not Venezuela. Typical *P. tibialis* is known only from Hispaniola and nearby Mona Island, and I hereby restrict the type locality to Hispaniola. Wolcott (1951) indicated that records of *tibialis* from Puerto Rico are erroneous. Some specimens from Mona I. have two very tiny yellow spots on the scutellum.

An extensively yellow maculated form of *P. tibialis* occurs on Great Inagua I. in the southern Bahamas. Bequaert (1948) described this as the "var. (or subsp.)" *barbouri*, and although still known only from a single female, the color pattern is so different from typical *tibialis* that I am recognizing it as a subspecies. Bequaert stated that the propodeal lamella of *barbouri* was "wavy, forming a broad upward curve midway between the lateral angle" and the metanotum. However, Bequaert's description of the lamella is misleading. It is abruptly angled midway, not "broadly curved." In most specimens of typical *tibialis* the lamella forms a broad, even curve from the tooth to the metanotum. Whether or not the angled lamella in the type of *barbouri* is the typical condition in this taxon, remains to be seen. If it is, then *barbouri* might be elevated to species as suggested by Bequaert, but on other structural grounds it seems conspecific with *tibialis*.

The female of *P. tibialis barbouri* differs from typical *tibialis* in having a completely yellow clypeus, a yellow stripe on the scape, yellow in the ocular sinus and a spot above the antennal sockets, an elongate yellow spot on the gena, a narrow yellow band along the hind margin of the pronotum (always ?), and two small yellow spots on the scutellum. The mesopleuron is largely yellow, and there is a round yellow spot on the propodeal side. Yellow on the propodeal dorsum extends broadly onto the hindface. The coxae and fore and midfemora have large yellow zones. Laterally the yellow bands on the gaster abruptly widen basad. The expansion on tergum I includes a fingerlike extension that is directed toward the midline. The expansion on tergum II is actually a narrowly discrete circular spot.

In contrast, typical *tibialis* is much darker. The clypeus is black on its apical one half or two thirds, and the scape, frons, and gena are entirely black. The pronotum is only yellow margined anteriorly, although some specimens show narrow traces of yellow posteriorly. The scutellum is usually black. The mesopleuron usually only has a tegula-sized yellow spot behind the pronotal lobe. Yellow is confined to the dorsum of the propodeum, and the coxae and femora are entirely black. The tergal and sternal bands are fairly uniform in thickness over their entire length.

The yellow genal spot of *barbouri* is suggestive of *scrupeus*, but the latter has extensive reddish brown coloration, a straight propodeal lamella, and punctuation in the black area of tergum I.

The narrowly yellow hindmargin of the pronotum in *barbouri* is similar to *guadulpensis*, but the latter has a fingerlike process over the mesopleural scrobe, and the propodeal lamella ends without forming a tooth or angle. It is possible that the degree of yellow maculation along the hindmargin of the pronotum varies in *barbouri*. This is suggested by the fact that a few females of typical *tibialis* show traces of yellow along the hindmargin.

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A DESCRIPTION OF THE LATE-INSTAR LARVA OF
XENOMYCETES LAVERSI HATCH (COLEOPTERA: ENDOMYCHIDAE)
WITH NOTES ON THE SPECIES' HOST AND DISTRIBUTION

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Abstract.—The late-instar larva of *Xenomycetes laversi* Hatch is described for the first time. SEM illustrations are presented to show unusual mycangial setae. *Paxillus atrotomentosus* (Batsch ex. Fr.) Fries is apparently the sole fungal host for both adults and larvae of the beetle. New collection data are presented for the species' known range in Washington and Oregon (New State Record).

Xenomycetes laversi Hatch was originally described from two specimens labelled "Seattle, Wash" (Hatch, 1961). Since this description, few specimens of this beetle have appeared in collections and no reports of it have been published. Here, I describe the late instar larva, identify the apparent sole host fungus, and report additional collections from various localities in western Oregon and Washington.

Larvae of six genera of Endomychidae found in North America have been described or illustrated. Böving and Craighead (1931) illustrated and gave key characters for *Mycetaea hirta* Marsham, *Aphorista vittata* (Fabricius), *Stenotarsus hispidus* Herbst, *Endomychus coccineus* Linnaeus., *E. biguttatus* Say, *Lycoperdina ferruginea* LeConte, and *Rhymbus ulkei* Crotch. Peterson (1960) provided illustrations of and a family description based on *L. ferruginea* and *E. biguttatus*. Pakaluk (1984) presented a description of the larva of *L. ferruginea* along with extensive biological data.

The following description is based on specimens which were killed in 70% ethyl alcohol, and preserved in a 19:1 solution of 70% ethyl alcohol and glycerin. Specimen preparation for SEM began with decapitation and a soaking in warm 1 N NaOH for 10-15 minutes. Specimens were then rinsed and flushed with distilled water, fixed with a solution of 2% glutaraldehyde in 0.1 M sodium phosphate, buffered, and dehydrated in a graduated series of ethyl alcohol. Specimens were then critical point dried, attached to stubs with double-stick cellophane tape, ion-coated with gold-palladium, and examined with an ISI-60 scanning electron microscope at 30 kv.

Xenomycetes laversi Hatch

Late instar larva.—Length 7.0 mm, width 1.8 mm, turgid; onisciform, broadly fusiform in dorsal aspect; shallowly convex dorsally; flavotestaceous, coriaceous, with sparsely to moderately distributed, erect, basket-like mycangial setae (Figs. 1, 3), marginal bristles slightly longer than discal bristles; densely set with truncate

microscoli (Figs. 4–5); terga and nota plate-like. Nota and terga 1–8 with an unsclerotized ecdysial suture densely set with truncate microscoli. Pleural and ventral regions cream colored, verrucose, densely set with truncate microscoli. Spiracles annular-uniform; thoracic spiracle on anterior portion of mesothorax; abdominal spiracles in pleural membrane on segments 1–8.

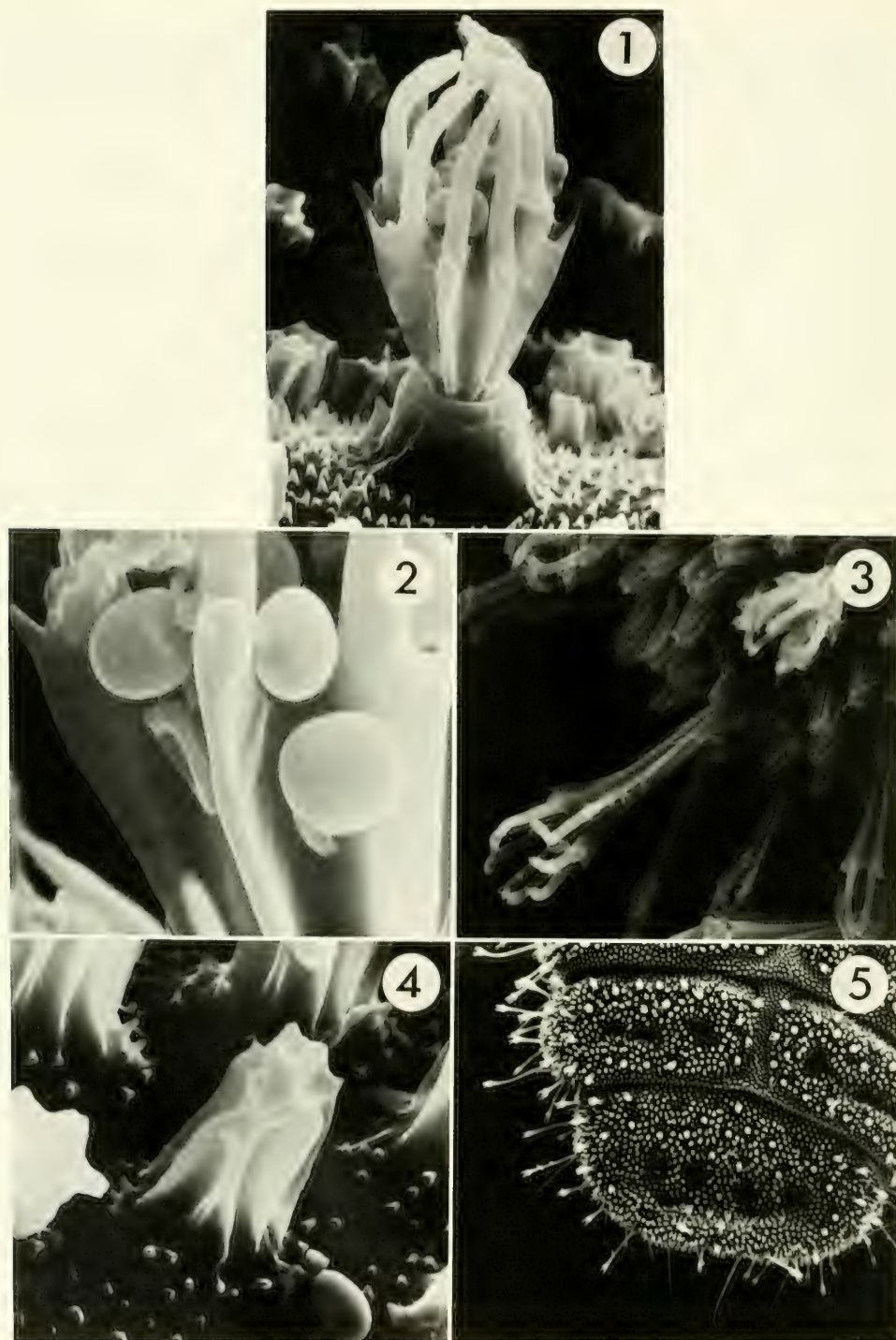
Head: $0.33\times$ as long as wide, $0.5\times$ as wide as pronotum, moderately well sclerotized; prognathus, slightly angled ventrally. Stemmata 3 each side, forming a nearly equilateral triangle. Ecdysial suture with frontal arms broadly U-shaped, epicranial stem absent. Antennae 3-segmented (Fig. 6), cylindrical; lateral sensorium trumpet-shaped, narrowing apically, slightly longer than segment 3. Mandibles (Fig. 7) slightly longer than wide; apically bifid, inner tooth with mesal preapical swelling; incisor lobe thin, blade-like mesally; prostheca flattened, membranous; molar lobe glabrous, developed as large, well sclerotized, serrate ridge. Labrum quadrate, slightly wider than long; anterior margin broadly shallowly emarginate. Epipharynx simple with medial, longitudinal asetose band; lateral portions with large acuminate setae directed medially, setae becoming minute laterally; anteriorly with setae forming whorled patches on disc. Labial and maxillary structures as in Fig. 8. Labial palps 2-segmented, set upon bulbous conjunctival membrane, apical segment short, cone-shaped. Maxillary palps short, 3-segmented; basal and second segments subequal in length and width; penultimate short, ring-like; apical segment $2\times$ longer than penultimate segment, broadly cone-shaped. Malae moderately sclerotized, lobate with a single large chitinous dentation medio-apically with 2–3 stout setae, an additional 7 of these setae extending basally on dorsal surface. Stipites not divided. Cardines triangular, weakly differentiated from stipites.

Thorax: Pronotum $2\times$ length of mesonotum, rounded trapezoidal, narrowing anteriorly in dorsal aspect; anterior lateral angles broadly rounded. Mesonotum and metanotum subequal in length, progressively slightly wider, metanotum $1.2\times$ width of pronotum. Legs of polyphagan type, sparsely set with long, acuminate hairs distad of coxa, without microscoli; coxa conical, slightly projecting; trochanter short triangular; femur fusiform; tibia $0.5\times$ as long as femur, subcylindrical; tarsungulus large, $0.5\times$ length of tibia.

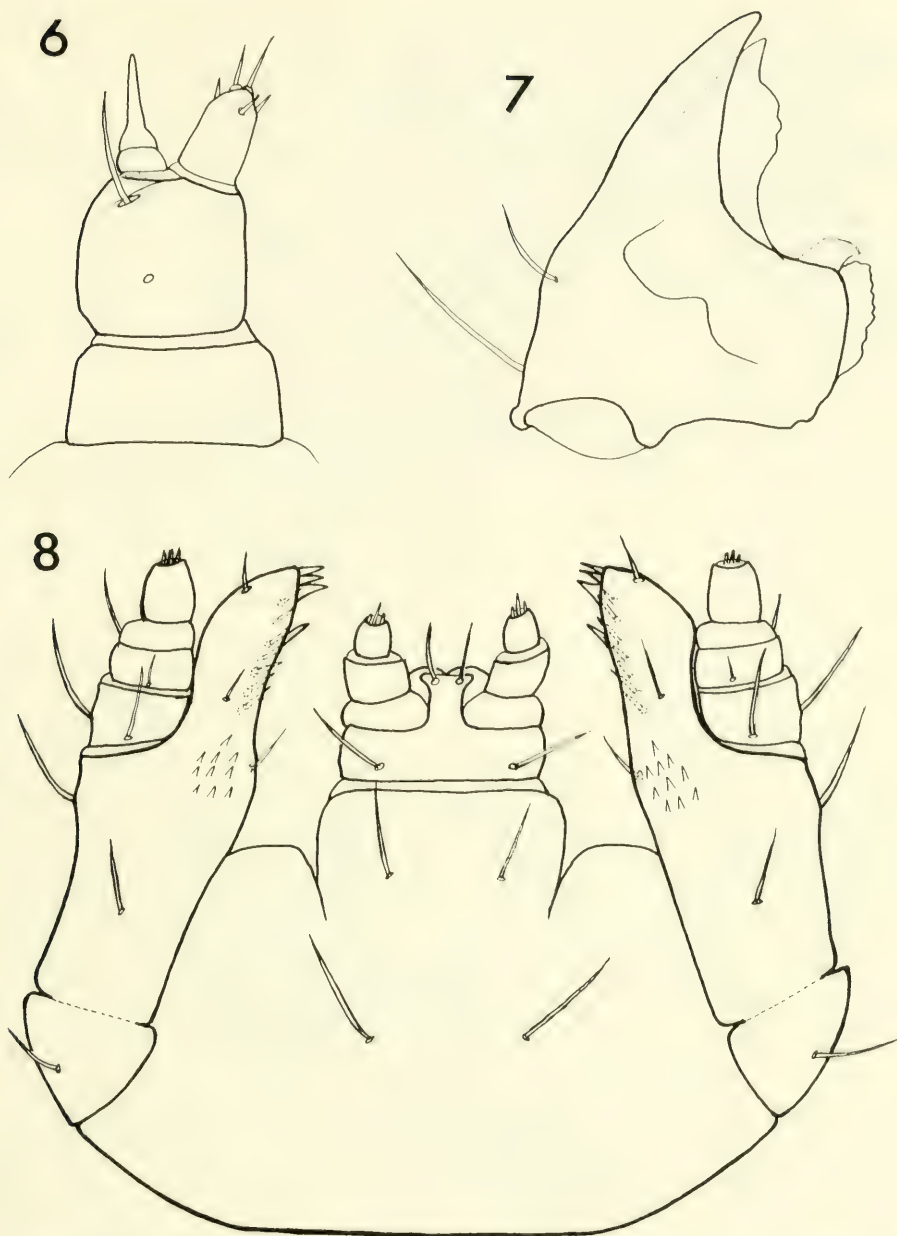
Abdomen: Terga similar to and subequal in width with metanotum to segment 5, then gradually, progressively decreasing in width to segment 9; segment 9 $0.5\times$ as wide as segment 1, and $1.5\times$ as long as segment 8, posterior margin evenly rounded; abdominal segment 10 obsolescent. Lateral margins of tergites broadly rounded, slightly oblique posteriorly. Anal region soft, extrusable; anal tube short, fleshy, unmodified, not forming a true pygopod.

Remarks.—With regard to the North American endomychid fauna, *X. laversi* larvae can only be confused with *Aphorista*, *Mycetaea*, and possibly *Endomychus* (see previous references). Discrimination of *X. laversi* from *Endomychus* and *Aphorista* is readily made by the lateral tergal projections and longer 2nd antennal segment of the latter genera; and from *Mycetaea* by its more deeply excavated incisor lobe of the mandible.

Mycangial setae (Figs. 1, 3) have apparently not been described in the larvae of Endomychidae or related families, although the phylogenetically related Coccinellidae often possess a variety of interestingly formed defensive spines. I have examined the larva of *Aphorista laeta* LeConte which possesses basket-like my-



Figs. 1-5. *Xenomycetes laversi* Hatch, late-instar larva. 1, Mycangial seta from disc of abdominal tergite, ca. 2000 $\times$. 2, Host fungus spores on mycangial setae, ca. 3000 $\times$. 3, Mycangial setae and microscoli on lateral-tergal region of abdominal tergite 7, ca. 1500 $\times$. 4, Tergal microscolus, ca. 2500 $\times$. 5, Dorsal posterior of larva, ca. 100 $\times$.



Figs. 6-8. *Xenomyces laversi* Hatch, late-instar larva. 6, Antenna. 7, Mandible. 8, Labium and maxillae, ventral aspect.

cangial setae very similar to those found on *Xenomyces*. Close examination of the illustrations of endomychid larvae by Peterson (1960), and Böving and Craighead (1931), suggest that similar setal formation may occur in *Aphorista vittata*, *Mycetaea hirta*, *Endomychus coccineus*, and *E. biguttatus*. These mycangial setae, as can be seen in Figs. 1-2, are evidently useful for the active transport of spores

of the host fungus, thus possibly permitting *X. laversi* larvae to act as distribution agents of the fungus.

Rawlins (1984) illustrates and briefly discusses cuticular modifications on the mycetophagous larva of *Epizeuxis lubricalis* (Geyer) (Lepidoptera: Noctuidae: Herminiinae) which closely resemble the truncate microscoli of *Xenomycetes* (Fig. 4). These structures were interpreted by Rawlins to be hydrophobic, useful for the prevention of integumental wetting and direct contact with host tissues and particles including pathogenic fungal spores. Rawlins also considered setal modifications to assist in the prevention of contact with detrital particles and rotted fungal tissues. These functions could also be important for *X. laversi* larvae, although SEM examination showed the occasional presence of fungal spores lodged between microscoli.

Xenomycetes laversi appears to be restricted to *Paxillus atrotomentosus* (Batsch ex Fr.) Fries (Basidiomycetina: Agaricales: Paxillaceae) in the classification by Singer (1975). All collections of the larvae, and most specimens of adults have been from sporocarps or mycelia of this fungus during the late summer to early winter months. In all situations, the fungus has been associated with the rotted wood of Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg., or mountain hemlock (*Tsuga mertensiana* (Bong.) Carr), in the form of stumps, logs, and limbs. *Paxillus atrotomentosus* is a saprobe of well-rotted conifer wood, especially *Pseudotsuga* and *Tsuga* (J. M. Trappe, pers. comm.), and is typically found in these woods at the late brown-rot stage of decay in which the wood has been delignified and forms elongate blocks. Singer (1975) lists *Pinus banksiana* Lamb. as a host for *P. atrotomentosus*, but this tree is not found in the known range of *X. laversi*. Miller (1978) indicates that this fungus is widespread and will fruit during both autumn and spring.

Larvae collected to date are apparently late instar. No earlier instar larvae or pupae have been reared or collected. Larvae have always been found with adults, some of the latter being teneral in late summer. Larvae and adults were observed grazing upon the basidia and mycelia. Occasionally, larvae have been found within tunnels in the cortex of the cap, but it is not known whether these tunnels were actually formed by the *X. laversi* larvae. Competition for food appears to be limited; few Collembola, Diptera larvae, or other mycetophagous Coleoptera have been observed on this fungus.

The known localities for *X. laversi* are within the low to mid-elevation hemlock forests of western Oregon and Washington. All of the localities are dominated by seral Douglas-fir or the closely related climax species of western and mountain hemlock. In addition to the type locality, the following records have been collated for this species (map, Fig. 9): WASHINGTON: Clallam County, Boulder Lake, Olympic Nat. Park, 21-VII-1953, M. C. Lane (1 adult, OSU); Skamania County, 10 mi. W Troutlake (Klickitat Co.), 3300 ft., 25-IX-1983, *Paxillus atrotomentosus*—caps & mycelia/buried mtn. hemlock wood, P. J. Johnson (4 larvae, 10 adults, PJJ). OREGON (NEW STATE RECORD): Benton County, Mary's Peak, 6-VI-1970, G. L. Peters (1 adult, GLP); 2500 ft., 9-II-1981, in pit trap near rotted Doug-fir log, P. J. Johnson (1 adult, PJJ); 1600 ft., Woods Creek road, 20-IX-1980, *Paxillus atrotomentosus*—cespitate caps on rotted Doug-fir stump, P. J. Johnson (3 larvae, 34 adults, PJJ); MacDonald State Forest, 4 mi. NW Corvallis, Sulfur Springs road, 6-III-1973, G. L. Peters (2 adults, GLP); 1-III-1978, under

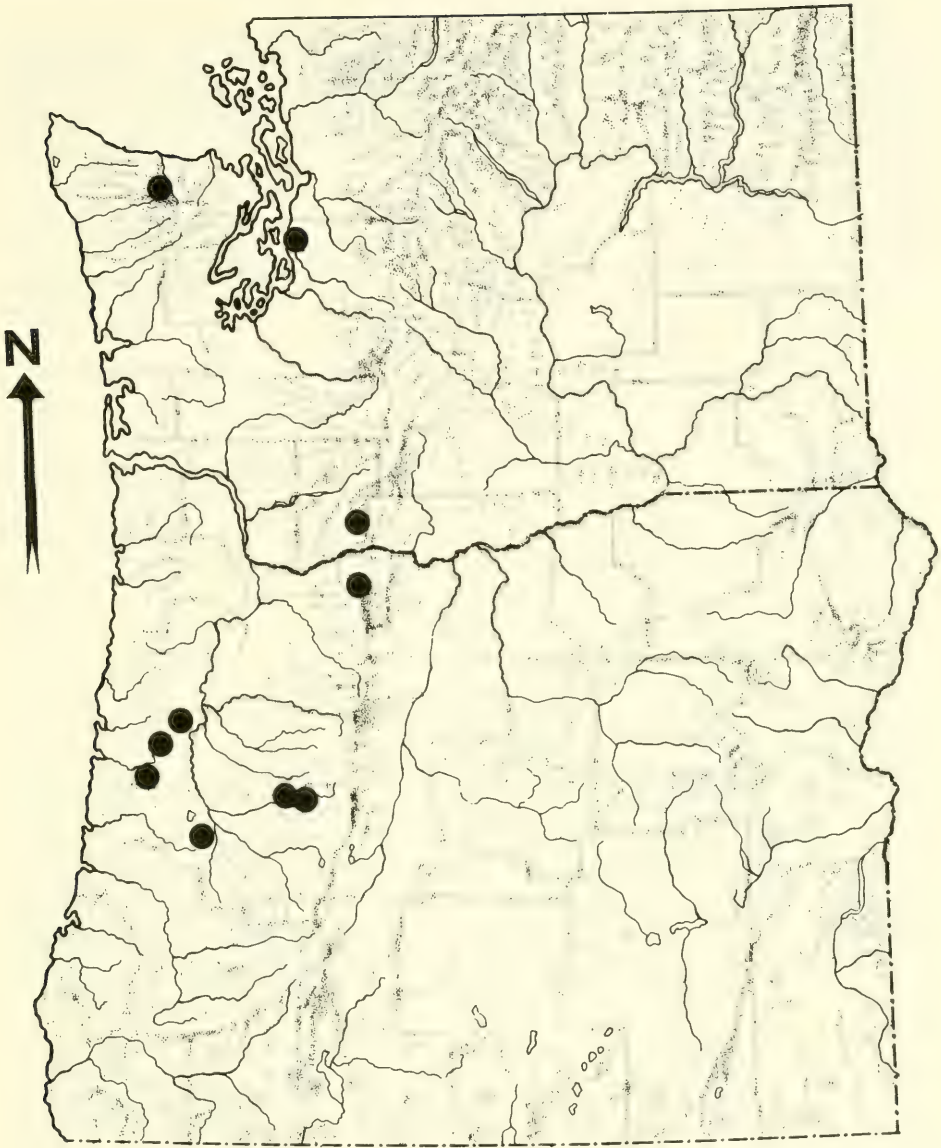


Fig. 9. Distribution of *Xenomycetes laversi* Hatch in Oregon and Washington; larva and adult records combined.

bark Doug. fir stump, P. J. Johnson (1 adult, PJJ); Oak Creek area, 22-III-1973, ex fungus on log, G. L. Peters (3 adults, GLP); 10-X-1978, ex under bark Doug-fir log (1 adult, GLP); Alsea Falls County Park, 7 mi. SW Alsea, XI-1979 (4 larvae, 7 adults, PJJ); 20-IX-1981, ex caps *P. atrotomentosus* (2 adults, PJJ); 10 mi. W Philomath, ex newt stomach, R. Friedburn (1 adult, OSU); Lane County, Spencer's Butte, Eugene, 13-X-1979, P. J. Johnson (4 larvae, 3 adults, PJJ); H. J. Andrews Exp. Forest, 6-VII-1979 (1 adult, OSU), 25-VII-1973 (1 adult, OSU), 10-VII-1972 (1 adult, OSU); Limberlost Campground, 5 mi. E. McKenzie Bridge, 3000

ft., 5-VII-1978, under bark rotted Doug-fir log, P. J. Johnson (1 adult, PJJ); Hood River County, Lost Lake, 2000 ft., 13-IX-1981, mycelia *P. atrotomentosus*/buried mtn. hemlock wood, P. J. Johnson (6 adults, PJJ). Collection abbreviations are: OSU (Oregon State University), GLP (G. L. Peters collection), PJJ (P. J. Johnson collection).

Larval specimens are located in the collections of the U.S. National Museum, Washington, D.C.; H. F. Strohecker, University of Miami, Coral Gables (collection now at Florida State Collection of Arthropods, Gainesville); J. F. Lawrence, CSIRO, Canberra; University of Idaho, Moscow; and my personal collection.

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**BIOLOGICAL NOTES AND DESCRIPTIONS OF THE IMMATURE
STAGES OF *PELASTONEURUS VAGANS* LOEW
(DIPTERA: DOLICHOPODIDAE)¹**

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Abstract.—*Pelastoneurus vagans* Loew is the most widespread species of its genus in North America. The immature stages inhabit mud substrates in a variety of aquatic and semiaquatic situations. Adults and larvae were collected from freshet seeps and mud flats in east-central Washington. The preferred habitats, third larval instar, larval mouthparts, pupa, and pupal cocoon are described and illustrated using line drawings and photographs.

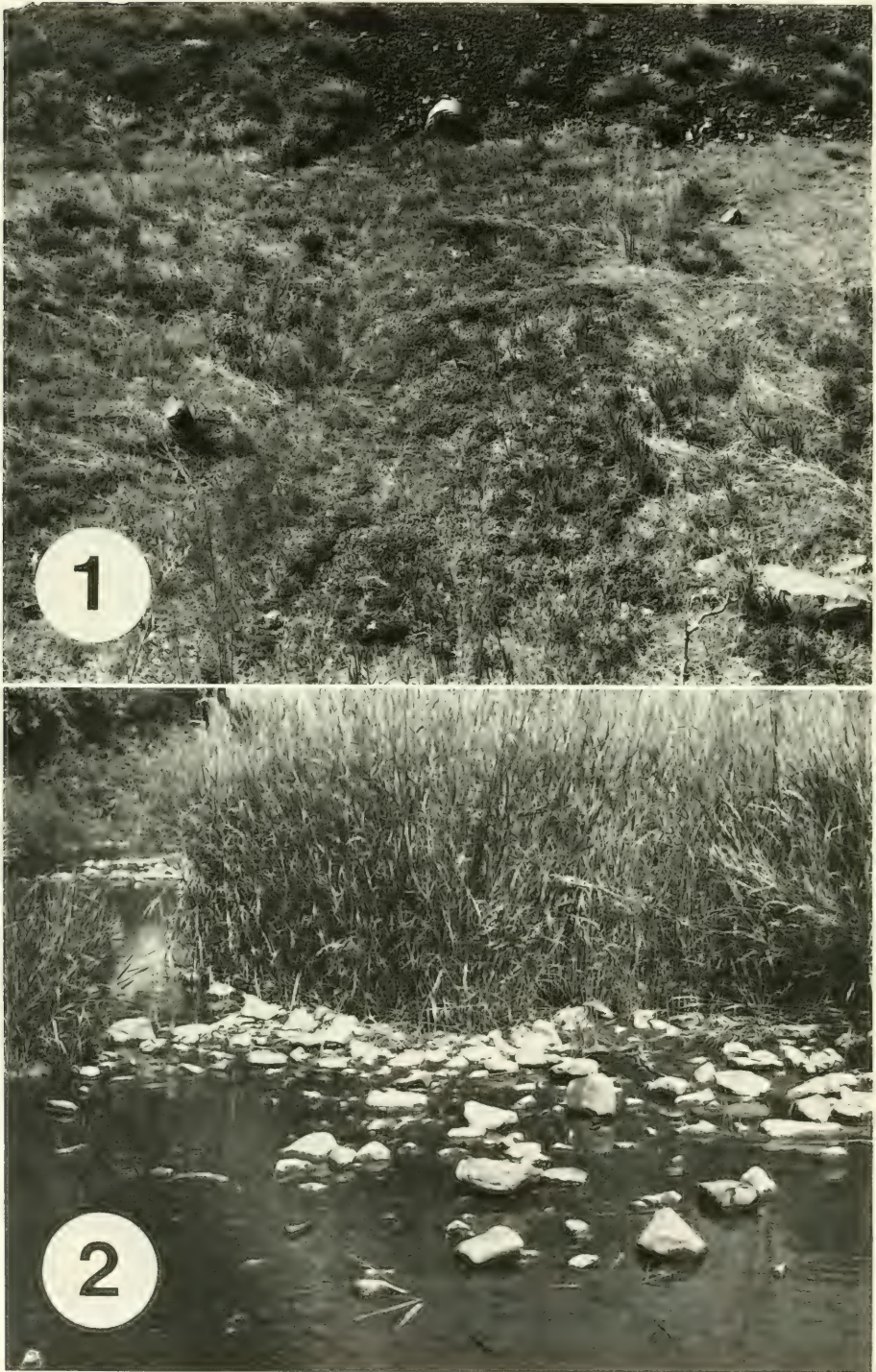
The Dolichopodidae represent an integral part of the insect fauna occupying many aquatic and semiaquatic habitats in North America. This study (Corpus, 1983) was an attempt to collect and identify the immature stages of some of the dolichopodids which frequent the freshwater seepages along the canyon walls of the Snake River and various mud flats in east-central Washington.

One of the most prevalent dolichopodids in these sites is *Pelastoneurus vagans* Loew, which has also been collected from roadside drainage ditches and waterfalls (Corpus, 1983). *Pelastoneurus* is represented by 29 Nearctic species, *P. vagans* being the most widespread (Foote et al., 1965). At present little biological information is available for any member of the genus.

MATERIALS AND METHODS

Several larval breeding sites of *P. vagans* were located after intensive surveys of the region revealed where adults occurred. Adults and larvae were collected from two sites in Whitman County in eastern Washington; Crum 4696, a seepage site 37.9 km SW of Pullman (Fig. 1), and Union Flat Creek at Klemgard County Park, 20.3 km W of Pullman (Fig. 2). Larvae of *P. vagans* were collected periodically throughout 1981 and 1982, beginning in late March and continuing into late August. To acquire larvae, substrate samples from both sites were collected and sieved through a series of Tyler standard testing sieves, numbers 8, 14, 20, and 35. Sieved soil from each screen was submerged in saline solution (150 mg NaCl/liter H₂O), causing the larvae to become active and float. Extracted larvae were rinsed in distilled water. Measurements of larvae and morphological struc-

¹ Scientific Paper Number 7372, Washington State University, College of Agriculture and Home Economics Research Center, Pullman. Work done under Project 0037.



Figs. 1, 2. Typical habitats of *Pelastoneurus vagans*. 1, Crum 4696. 2, Union Flat Creek.

tures were made using an ocular micrometer in a dissecting microscope. In addition to measurements, observations were also made of active larvae in the laboratory.

Larvae to be used for identification were placed into Kahle's solution for 12 hours and then transferred to 70% ethanol. For subsequent analysis, larvae were later cleared in 10% KOH. Live larvae were placed into petri dishes of freshly screened mud for subsequent development to adults. All larvae extracted for rearing during each period were placed in a common petri dish. Each petri dish thus corresponded to a separate sampling period. Chironomid larvae extracted from other samples were added as prey, and each rearing dish placed under a 16L:8D photoperiod regime. Seventy-four rearing dishes were set up in this manner, 44 with specimens taken at Crum 4696 and 30 from Union Flat Creek. Dishes were checked daily. Newly emerged adults were aspirated, identified, and pinned. Intact pupae and pupal exuviae were placed into 70% ethanol. Pupal cocoons were removed, air dried, and sprayed with hair spray to retain their structure for later description. Descriptions and terminologies follow those of Dyte (1967), Beaver (1966), and Smith (1952).

LIFE HISTORY OBSERVATIONS

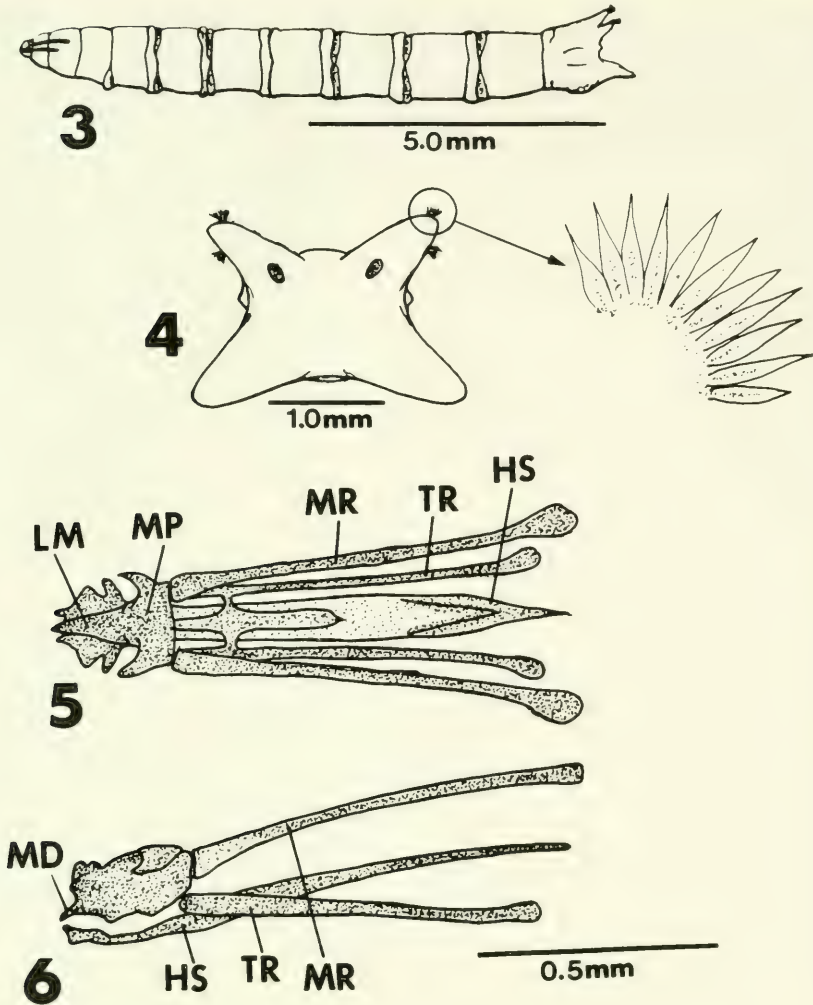
The developmental period from first larval instar to adult for *P. vagans* was 22–30 days ($n = 10$; $\bar{x} = 24$). Larvae remained within the mud media throughout their development. Developmental periods for pupae varied from 4–7 days ($n = 8$; $\bar{x} = 6$). Pupae could be detected in the rearing dishes by viewing the mud under the dissecting microscope to locate respiratory horns of the cocoons protruding 1–2 cm above the mud surface. When touched, these horn tips would move in a scissoring fashion, and on one occasion were drawn beneath the mud surface, presumably back into the cocoon. On occasion, more than one pupa was found and extracted from the same vicinity in a rearing dish, suggesting that pupae may share cocoon sides when adjacent to one another, and that larvae may have site preferences in which to pupate. Pupal exuviae were always found plugging the cocoon exit holes, indicating that adults always emerged at the surface of the mud directly above their pupal cocoons.

Newly emerged adults were never observed feeding in the laboratory, although they regularly imbibed water from the mud surface. Adult longevity, under laboratory conditions, was 3–5 days ($n = 8$; $\bar{x} = 4.1$). During the extraction process, several unidentified species of other dipteran larvae were collected including tipulids, ephydriids, and chironomids. During surveys at the two field sites several other dolichopodid species were collected, including *Tachytrechus auratus* (Aldrich), *T. olympiae* (Aldrich), *Rhaphium pollex* (Van Duzee), *Chrysotus arcuatus* Van Duzee, *C. argentatus* Van Duzee, and *Syntormon tricoloripes* Curran.

DESCRIPTIONS OF IMMATURE STAGES

Egg.—Length 0.6–0.7 mm; width 0.3–0.4 mm; ovoid; whitish; chorion appearing finely pebbled. (Based on 38 eggs, dissected from five females having 6, 6, 8, 9, and 9 eggs, respectively.)

First larval instar.—Length 1.3–1.7 mm; maximum width 0.23–0.35 mm; 12-segmented; metapneustic; translucent to white; mouth parts black; dorsolateral

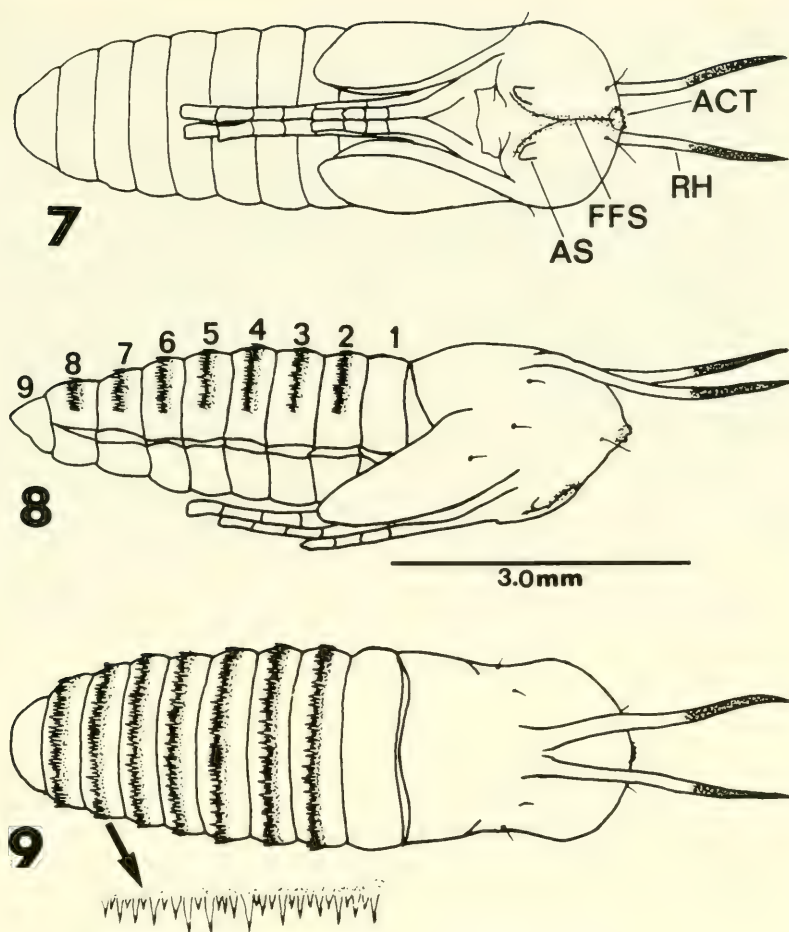


Figs. 3-6. *Pelastoneurus vagans*. 3, Larva, lateral view. 4, Posterior spiracular disc, segment 12, with enlarged hair tuft. 5, Larval mouth parts, dorsal view. 6, Same, lateral view. Abbreviations: (HS) hypopharyngeal sclerite. (LM) labrum. (MD) mandible. (MP) median plate. (MR) metacephalic rod. (TR) tentorial rod.

and ventrolateral lobes short, equal in length; posterior spiracles indistinct, located near tips of dorsoventral lobes. (Based on 2 larvae and 2 larval exuviae.)

Second larval instar.—Length 4.3–5.7 mm; maximum width 0.61–0.66 mm; 12-segmented; white; mouth parts black; amphineustic; anterior spiracles on segment 2; posterior spiracles on posterior spiracular disc of segment 12, blackish, borne near bases of dorsolateral lobes; dorsolateral lobes of segment 12 shorter than ventrolaterals. (Based on 2 larvae and 3 larval exuviae.)

Third larval instar (Fig. 3).—Length 9.6–10.3 mm; maximum width 1.5–1.7 mm; 12 segmented; whitish; mouth parts dark brown to black; body tapered anteriorly, truncate posteriorly; integument finely striate along lateral line and on venter; segment 1 retractile; body segments 4–11 with obvious ventral creeping



Figs. 7-9. *Pelastoneurus vagans*. 7, Pupa, ventral view. 8, Same, lateral view. 9, Same, dorsal view with enlargement of spinule row of 7th abdominal segment. Abbreviations: (ACT) apical cephalic tubercle. (AS) antennal sheath. (FFS) frontal facial suture. (RH) respiratory horn.

welts composed of transverse rows of minute setulae and recurved, triangular, cuticular protuberances. Amphineustic; anterior spiracles on segment 2, stalked, 0.03 mm long; posterior spiracles dark brown, located at bases of dorsolateral lobes, 0.49–0.53 mm apart, each 0.13–0.15 mm diam.; posterior spiracular disc of segment 12 (Fig. 4) with 6 projecting lobes, 2 dorsolateral, 2 very short lateral, and 2 ventrolateral; each dorsolateral lobe with 2 hair tufts, each tuft comprised of 8–12 hairs that appear to be widened basally; perianal pad on venter of segment 12 large, longitudinally rugose, ovoid in shape. (Based on 12 larvae.)

Larval mouth parts (Figs. 5, 6).—Labrum with acute tip, appears to curve ventrally near apex; arms of median piece project laterally, curve forward near tips; hypopharyngeal sclerite 0.65–0.71 mm long, caudal tip acute, amber; metacephalic rods broadly spatulate at caudal tips, curved laterally, 0.87–0.91 mm long; tentorial rods 0.70–0.75 mm long, caudal tips spatulate, slightly curved laterad, black. (Based on 3 head capsules.)

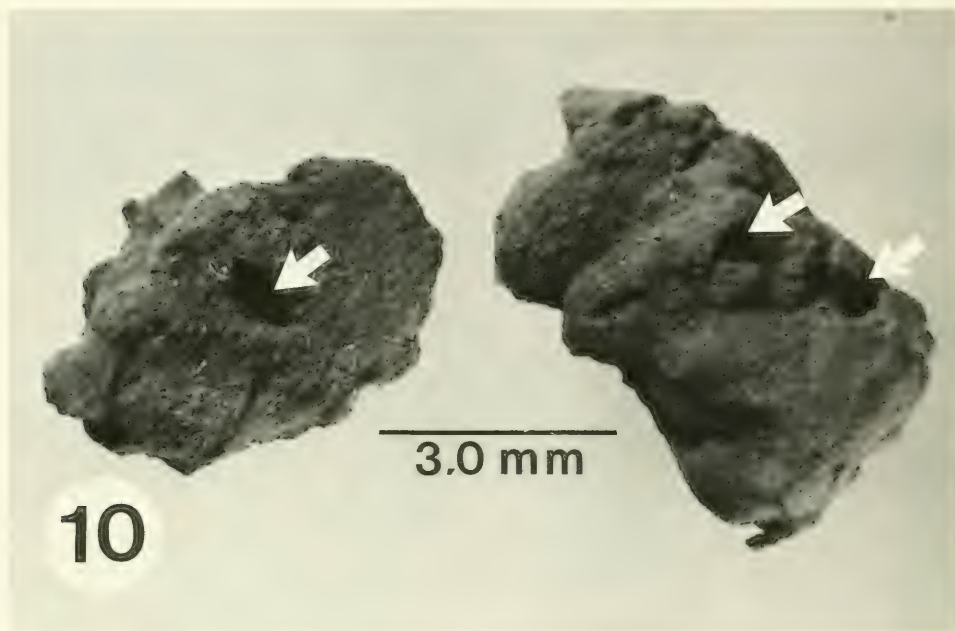


Fig. 10. *Pelastoneurus vagans*. 10, Pupal cocoons with emergence holes (arrows).

Pupa (Figs. 7, 8, 9).—Total length 4.9–5.2 mm from abdominal tip to apical cephalic tubercle; thorax in dorsal view 1.8–2.0 mm wide; prothoracic respiratory horns 1.7–1.9 mm long; body amber; sutures, tubercles, respiratory horn bases, and distal one-half of horns dark brown. Respiratory horns directed forward, slender, slightly curved, unsegmented, terminating in sharp points. Frontofacial sutures 0.70–0.75 mm long, resemble inverted “Y,” diverge below antennal sheaths; apical cephalic tubercles with four blunt points; a single seta 0.19–0.20 mm long on each side. Thoracic dorsum with three setae on each side of midline; pedothecae 1 reach posterior edge of first abdominal segment and pterothecae; pedothecae 2 reach posterior edge of fourth abdominal segment; pedothecae 3 reach edge of fifth abdominal segment. Abdomen 9-segmented, slightly curved, blunt posteriorly, dorsal surface of segments 2–8 with transverse spiniferous bands, each consisting of close-set row of brown spines directed posteriorly, increasing in size mesally. (Based on 3 intact pupae and 14 pupal exuviae.)

Cocoon (Fig. 10).—6.0–7.2 mm long; 4.2–4.8 mm wide; irregularly shaped; composed of fine soil particles; color dark chocolate brown when fresh; inner surface smooth; outer surface pebbled; adult emergence hole 1.5–2.1 mm diam. (Based on 14 cocoons.)

ACKNOWLEDGMENTS

I thank R. D. Akre, E. P. Catts, J. W. Crane, and R. S. Zack for their advice during this research. Appreciation is extended to R. D. Akre and E. C. Klostermeyer for providing funding for this project.

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NEW RECORDS FOR *XYLOSANDRUS* AND *XYLEBORUS* SPECIES (COLEOPTERA: SCOLYTIDAE)

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Abstract. — *Xyleborus validus* Eichhoff, *X. tachygraphus* Zimmermann, and *Xylosandrus crassiusculus* (Motschulsky) are reported from Louisiana for the first time, and the latter two species are new state records for Arkansas and Florida, respectively. *Xyleborus planicollis* Zimmermann is also a new state record for Arkansas. Additional locality and host records are given for *Xylosandrus compactus* (Eichhoff), *X. germanus* (Blandford), *Xyleborus obliquus* (LeConte), and *X. lecontei* (Hopkins).

Four introduced scolytids have been collected in Louisiana in recent years including *Xyleborus validus* Eichhoff and *Xylosandrus crassiusculus* (Motschulsky), which are reported from the state for the first time. A new Florida state record is given for the latter species. The first records of *Xyleborus planicollis* Zimmermann and *X. tachygraphus* Zimmermann in Arkansas and for the latter species in Louisiana are also given. Additional locality and host records are reported for *Xylosandrus compactus* (Eichhoff), *X. germanus* (Blandford), *Xyleborus obliquus* (LeConte), and *X. lecontei* (Hopkins).

The black twig borer, *X. compactus*, is probably of southeast Asian origin according to Wood (1977). He (1977, 1982) reported its occurrence in Florida in 1941, in Mississippi in 1968, and in Georgia, possibly in 1975. In Louisiana, this species was first collected in twigs of *Magnolia grandiflora* L. in New Orleans on May 6, 1976 (Cancienne, 1976a) and later that year from Jefferson and St. Tammany Parishes (Cancienne, 1976b). Oliver (1978) reported infestations in two additional parishes and reviewed its life cycle and economic importance. In addition to the ones from New Orleans, specimens were examined from the following five parishes: Ascension, Prairieville, 13-X-1977; Beauregard, 5 mi. S DeRidder, March 25, 1982 (EGR); East Baton Rouge, Baton Rouge (21-XI-1977; Place DuPlantier Apts., 13-III-1984, flight trap; 17-IV-1984, em. from *Koelreuteria paniculata* [male]); Point Coupee, 10-V-1978, boring in pecan trunk (male); and St. Tammany, Pearl River, 29-VII-1976; four of these records are from *M. grandiflora*. In 1976, this species was also reported for the first time in Mobile and three other counties in Alabama (McQueen, 1976) and in North Charleston, South Carolina, and later from other localities in the latter state (Hardee et al., 1980). Dixon and Woodruff (1982) discussed its distribution, hosts, and biology in Florida.

Xylosandrus germanus, described from Japan, was first reported from the United States in 1932; it presently occurs from Connecticut south to Georgia and west to Missouri and Louisiana (Bright, 1968; Weber and McPherson, 1982a; Wood, 1977, 1982). This species was first collected in the state on May 10, 1978, when adults emerged from a pecan tree trunk in a small orchard at Morganza in Pointe Coupee Parish (Chapin, 1978). Specimens were also collected in Baton Rouge, East Baton Rouge Parish, on May 2, 1982, emerging from the trunk of a satsuma var. Kimbrough. This is a new host and locality record (Weber and McPherson, 1982a, 1983). Other specimens were collected at Place Duplantier Apartments in Baton Rouge on March 15 and 24, 1984 and on March 10 and 14 and April 27, 1985. Most of them were caught in a window trap (EGR).

An earlier record of the occurrence of *X. germanus* in Indiana was apparently overlooked by Weber and McPherson (1982a, 1982b, 1983). It was reported for the first time from river birch in Dubois County in 1964 (USDA, 1964).

Anderson (1974) reported the first United States record for *Xyleborus semio-pacus* Eichhoff based on specimens taken from a sweetgum graft at Summerville, in Dorchester County, South Carolina. In 1975, he pointed out that the scientific name should be *X. crassiusculus* (Motschulsky) according to Wood (1969). Wood (1977, 1982) placed the species in *Xylosandrus* and gave the probable area of origin as southeast Asia. This species was also reported on plum in Richmond County, North Carolina (Hunt, 1979), and from sweetpotato in Marion County (Kissam, 1979) and cherry in Charleston County (Wood, 1982). Specimens were collected from the trunk and main limbs of a Japanese persimmon tree, *Diospyros chinensis* Blume, in Baton Rouge on May 24, 1980, by L. D. Newsom.

Adults were collected from March 9 to July 25, in September, and on December 21 in the following 9 parishes: Caddo, Gilliam; Catahoula, Sicily Island Hills Wildlife Management Area; East Baton Rouge, Baton Rouge (em. from trunk of satsuma tree, var. Kimbrough; em. from *Koelreuteria paniculata*; LSU campus; Place Duplantier Apartments [LSUC; EGR]); East Feliciana (Camp Avondale, 3 mi. E Clinton; Idlewild Research Station, Clinton [LSUC, EGR]); Livingston, Watson, dug from peach tree branch; Natchitoches (Kisatchie National Forest nr. Red Bluff Campgrd.; Red Bluff Campgrd.; Red Dirt Wildlife Management Area; Little Bayou Pierre at LA Hwy. 118); Plaquemines, Citrus Research Station, Port Sulphur, boring in peach tree; St. Landry, nr. Opelousas, Louisiana Nursery, *Magnolia soulangeana*; and West Feliciana (2 mi. W. Jackson, Vaughns Bayou [EGR]; Tunica Hills W of Weyanoke). Specimens were collected at lights, black light, mercury vapor and black lights, flight traps, window traps, and occasionally by sweeping.

The first record of this species in Florida is based on a specimen collected in Torreya State Park in Liberty County on April 11, 1983 by E. G. Riley.

Xyleborus validus, which occurs in northern Japan, became established in New York about 1975 and was reported from Pennsylvania in 1980 (Wood, 1977, 1982). In Louisiana, the first specimens were collected in the Thistlethwaite Wildlife Management Area in St. Landry Parish on June 1, 1984, emerging from *Acer negundo* L. Other records include three additional parishes: East Baton Rouge, Baton Rouge (LSU campus, 8-III-1985, mercury vapor and black light; 15-IV-1985, in *Wisteria* sp.; Place Duplantier Apartments [IV-29-83, March 13, 22, 24,

April 23, and July 21, 1984, window trap; 14-III-1985 (EGR)]; Orleans, New Orleans (3-VI-1985; City Park, 9-VII-1985; both emerged from *Koelreuteria paniculata* Laxmann); and West Baton Rouge, Hwy 415 at I-10, 17-IV-1985.

Additional records, which extend the range or provide more detailed locality data, are given below for four other *Xyleborus* species.

Xyleborus obliquus (LeConte) was reported from New Iberia by Bright (1968). Louisiana was omitted from the distribution records in Wood (1982), and this locality was mistakenly included in the Virginia list. Specimens were collected in Baton Rouge from March 15 to April 19, on August 31 and on December 21, and at Idlewild Research Station near Clinton in East Feliciana Parish in April (EGR, LSUC).

Xyleborus lecontei (Hopkins) was reported from the "Delta area" by Wood (1982). Two specimens emerged from dead limbs collected March 11, 1982, by E. G. Riley on Grand Chenier in Cameron Parish. One of these emerged from *Acacia farnesiana* (L.) Wild. (Fabaceae: Mimosoideae).

The following two specimens of *Xyleborus tachygraphus* Zimmermann were examined: Arkansas, Montgomery Co., R.27W., T.4S., Sec. 32, 2-IV-1980, C. B. Barr (LSUC); Louisiana, East Baton Rouge Parish, Baton Rouge, Place Duplantier Apts., 16-III-1983 (EGR). These represent new state records and extend the range of this species westward from Illinois and Alabama (Wood, 1982).

A specimen of *X. planicollis* Zimmermann, bearing the following label data, was collected for the first time in Arkansas: Polk County, S of Board Camp R29W, T3S, SE Sec. 22; 2-4-IX-1984; MV & BL, Coll. C. B. & J. E. Barr. This species was reported from Missouri, Indiana, and Pennsylvania by Wood (1982).

Specimens of *X. affinis* Eichhoff, *X. celsus* Eichhoff, *X. ferrugineus* (F.), and *X. pubescens* Zimmermann from Louisiana were also examined, and *X. xylographus* (Say) may occur in the state.

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TEN-YEAR SUPPLEMENT TO "ANT LARVAE: REVIEW AND SYNTHESIS"

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Abstract.—A previous review and synthesis of published information on ant larvae is brought up to date. The same general format as the earlier review is used to relate them more readily to users.

Since our Memoir No. 7 "Ant Larvae: Review and Synthesis" was published in 1976, we have studied the larvae of 20 genera and 85 species. So much new material necessitates a partial revision, the purpose of this supplement. We have followed the same plan as in Memoir 7 and also given page references, so that any part of one may be quickly related to the corresponding part of the other. Three new topics have been added: Importance of Larvae, Changes in Nomenclature, The Future.

AVE ATQUE VALE (p. 1)

In paragraph 2 change 850 to 986 and 475 to 825.

Change paragraph 3 (in part) to read: "... it has appeared in 67 papers scattered through 15 journals over a period of 58 years ..." Add 3 journals: American Entomological Society, Transactions (5); Australian Entomological Society, Journal (1); New York Entomological Society, Journal (3). Change *Psyche* to 16 and Journal of the Kansas Entomological Society to 2.

HISTORY (p. 1)

In our chapter on "Larvae of Social Insects" (1979a) we used material and figures from Memoir 7 (1976). In a key (1979a: 315 and 1979b: 10) we separated for the first time ant larvae from those of other social insects:

- 1a. Larvae not reared separately in cells but together in nest chambers; hairs usually conspicuous on head and body 2
- 1b. Larvae reared in separate cells; hairs none or few and minute; temporal sulci present; antennae nearly always at or below lower third of cranium 3
- 1c. Larvae reared in separate cells; hairs few and minute; temporal sulci absent; antennae at lower third of cranium *Microstigmus comes*
- 2a. Body J-shaped; anterior half stout and strongly curved ventrally; posterior half straight and tapering to a sharp point; temporal sulci present; antennae usually on lower third of cranium ... Allodapoid Anthophoridae

- 2b. Body any one of diverse shapes but never as above; temporal sulci absent; antennae usually on upper half of cranium Formicidae
- 3a. Body straight; diameter greatest at AI and AII; gradually attenuated toward posterior end and more rapidly toward anterior end; each in a separate cell of a paper comb; usually hanging head down Vespidae
- 3b. Body stout, not straight; not in separate cells 4
- 4a. Thorax and AI bent ventrally; abdomen straight and of nearly uniform diameter; opening of sericteries without lips; nests in soil or rotten wood; cells lined with wax Halictidae
- 4b. Body crescentric; opening of sericteries with conspicuous lips; cells constructed of wax or of a mixture of wax and pollen Apidae

HISTORY AND METHODS (p. 1)

We now prefer 70% alcohol. If tax-free alcohol is not available, rubbing alcohol (ethyl but *not* isopropyl) may be used.

Drawing (p. 1).—Line drawings are not difficult to make: see our 1960a. Inking, however, does require more skill, which can be acquired with practice. We now use polyester drafting film, India ink for film and Rapidograph drawing pens for film (sizes 000, 0 and 1); the Hunt mapping pen is still good for details such as hairs on the body. The great advantage of film is that errors can be erased or carefully scraped off with a knife. French curves are useful but—as usual—must be carefully fitted to the desired curve.

The Scanning Electron Microscope (p. 1).—Photographs made by a scanning electron microscope (SEM) are now popular, although their use sometimes appears to be superfluous. In this regard, we cite the article by Clark and Glavog (1976: 1361). SEMs are especially useful when it is desirable to magnify higher than can be done with a light microscope, e.g. surface features of the integument. We find that any whole larva or any detail that can be seen under a light microscope can be shown more clearly with a photomicrograph or a line drawing. An example of the superiority of line drawings over SEMs is to be found in Kempf (1975).

LITERATURE (p. 1)

As the next-to-last sentence in the first paragraph insert “They total 1298.”
In the last line change 577 to 632.

MATERIAL STUDIED (p. 1)

We have studied the larvae of 777 species in 202 genera representing 51 of the 61 tribes and all 10 of the living subfamilies. The taxa are given in Appendix B. A summary by subfamilies of the number of genera and species (in parentheses) follows: Dorylinae 6 (23); Leptanillinae 2 (3); Cerapachyinae 5 (11); Myrmeciinae 2 (31); Ponerinae 41 (169); Pseudomyrmecinae 4 (34); Myrmicinae 94 (299); Aneuretinae 1 (1); Dolichoderinae 14 (54); Formicinae 33 (154).

GEOGRAPHICAL DISTRIBUTION (p. 2)

Additions only.—AFRICA—Angola 2, Cameroon 2, Ghana 3, Ivory Coast 5, Kenya 3, Madagascar 5, Morocco 1, South Africa 2, Tunisia 1, Zambia 1.
ASIA—India 4, Japan 3, Malaya 1, Singapore 1.

AUSTRALIA—New South Wales 2, South Australia 1. (It is significant that our supply of larvae has been greatly reduced as a result of Australia's restrictions on export of scientific material and the red tape attendant thereon.)

CENTRAL AMERICA—Costa Rica 9, Panama 1.

EUROPE—Spain 2.

MALAY ARCHIPELAGO—Borneo 6, Celebes 9, New Guinea 2, Philippines 1, Indonesia 1.

OCEANIA—New Hebrides 1.

SOUTH AMERICA—Brazil 15, Chile 3, Colombia 2, Ecuador 3.

UNITED STATES—Alabama 2, Florida 3, Texas 2.

WEST INDIES—Guadelupe 1.

MORPHOLOGY (pp. 2–45)

Color (pp. 4–5)

Under "green" add: *Leptothorax obturator* "a peculiar greenish tint."

Body Shape (p. 8)

On page 8 after the third line insert: ADVICE.—We recommend that in descriptions of ant larvae the profile type and mandible shape be followed by our definition of that type or shape, e.g., "Larvae pheidoloid (i.e., abdomen short, stout and straight; head ventral near anterior end, mounted on a short stout neck, which is the prothorax; ends rounded, one more so than the other." It is insufficient and inaccurate to say "like *Pheidole*": that is merely the derivation of the term.

Page 8. 1. POGONOMYRMECOID—Add *Mystrium*, *Plectroctena* to PONERINAE and delete *Stigmatomma*. Add to MYRMICINAE: *Eutetramorium*, *Goniomma*, *Hylomyrma*, *Lordomyrma*, *Octostruma*, *Terataner*; delete *Colobostruma*, *Dilobocondyla*. Add to FORMICINAE: *Acantholepis*, *Acropyga*, *Colobopsis*, *Cataglyphis*, *Proformica*, *Teratomyrmex* and change *Plagiolepis* to *Anoplolepis*.

2. PHEIDOLOID—Under MYRMICINAE add *Antichthonidris*, *Ochetomyrmex*; delete *Oligomyrmex* and *Paedalgus*. Under FORMICINAE add *Aphomyrmex*, *Petalomyrmex*. Delete DOLICHODERINAE: *Engramma*.

3. DOLICHODEROID—Add to definition "diameter approximately half the distance from labium to anus." Add *Engramma* and *Turneria* to DOLICHODERINAE; change *Dorymyrmex* to *Conomyrma*.

4. ATTOID—Change definition to read: "Short, very stout, plump, slightly curved, with both ends broadly rounded; anterior end formed by the enlarged dorsum of prothorax; head ventral, near anterior end; no neck; somites indistinct; diameter approximately equal to distance from labium to anus." Occurrence.—MYRMICINAE: *Nothidris*, *Proatta* and tribe Attini.

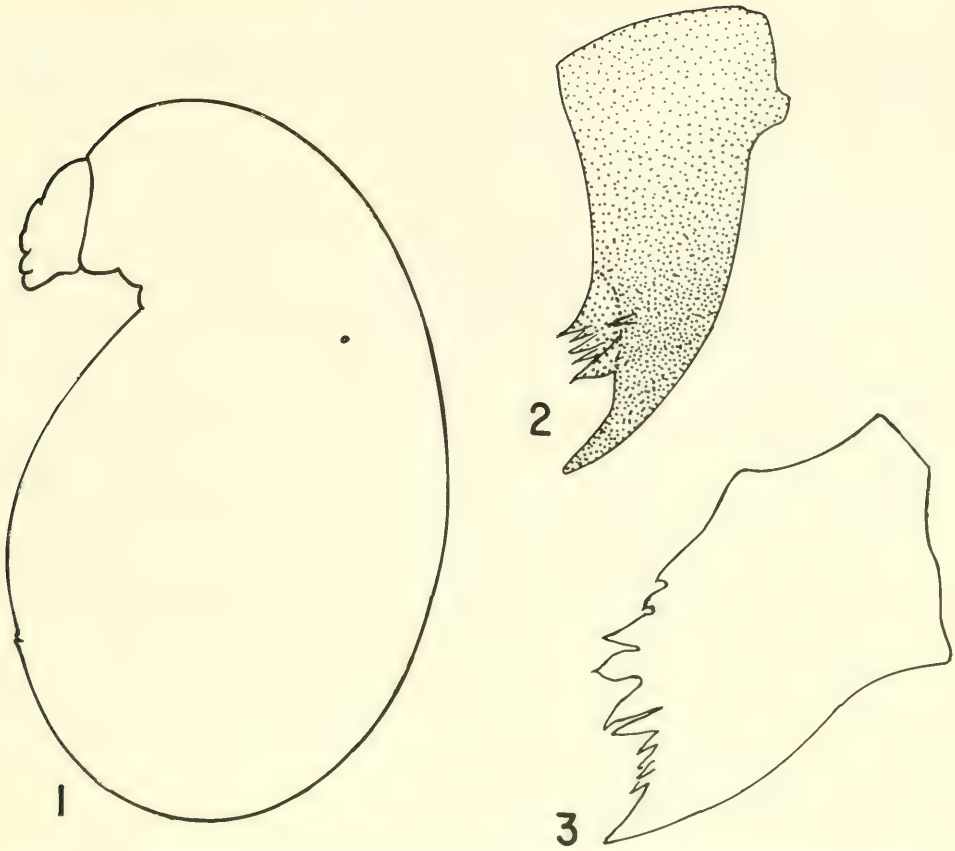
5. MYRMECIOID—MYRMECIINAE: Add *Nothomyrmecia*. PONERINAE: Add *Apomyrma*. MYRMICINAE: Add *Adlerzia*.

6. CREMATOGASTROID—Change *Cryptocerus* to *Zacryptocerus* under MYRMICINAE.

7. APHAENOGASTROID—MYRMICINAE: Add *Basiceros*, *Colobostruma*, *Oxyopomyrmex*; delete *Novomessor*.

8. PLATYTHYREOID—Delete *Eubothroponera*.

11. OECOPHYLLOID—Add *Acantholepis*.



Figs. 1–3. Paedalgoid profile type to be added to Fig. 3. Figs. 2 and 3. Mandible shapes to be added to Fig. 20. 2, *Ochetomyrmecoid*. 3, *Simoponoid*.

12. RHOPALOMASTIGOID—Add *Melissotarsus*.

A NEW PROFILE TYPE 13. PAEDALGOID—Abdomen subspherical; thorax forming a stout very short neck, which is directed ventrally; anus ventral, quite far forward and with a posterior lip. Occurrence.—MYRMICINAE: *Oligomyrmex*, *Paedalgus*. Add Fig. 1 to Fig. 3 in Memoir 7.

Body Hairs (p. 22)

Insert the following as the first paragraph under “Classification of hair-types”: “If both larval and adult stages are taken into account, then ants and bees are the only major groups of aculeate Hymenoptera in which complex hairs are abundant” (Lanham, 1979:91).

Under I. A. 3. UNCINATE. MYRMICINAE: add *Basiceros*, *Octostruma*.

Under I. A. 4. ANCHOR-TIPPED change 28 to 31 in last line.

Under I. A. Add “5. FLEXUOUS SHAFT AND FAN-SHAPED TIP (about 0.37 mm long). Occurrence: MYRMICINAE—*Hylomyrma*. (See 1977: 587.)”

Under II. A. 1. c. Add at end *Ochetomyrmex*.

Labrum (pp. 36–37)

CHIOSCLERES—Add to last sentence: “in the Formicinae and *Mystrium* and *Simopelta* in Ponerinae.”

Mandibles (p. 38)

On page 39 under SHAPE:

1. ECTATOMMOID—Delete Myrmeciinae: *Myrmecia*. Add to PONERINAE: *Myopopone*, *Plectroctena*. Add to MYRMICINAE: *Antichthonidris*, *Basiceros*, *Eutetramorium*, *Goniomma*, *Lordomyrma*, *Nothidris*, *Terataner*; change *Cryptocerus* to *Zacryptocerus*. Add to FORMICINAE: *Proformica*.

2. CAMPNOTOID—2nd line, change first clause to read “forming a round-pointed slightly curved tooth.” Add to FORMICINAE: *Acantholepis*, *Acropyga*, *Aphomomyrmex*, *Cataglyphis*, *Colobopsis*, *Petalomyrmex*, *Teratomyrmex*.

3. DOLICHODEROID—2nd line, first half, change to read “distal part, which is slender, sharp-pointed and straight.” Delete *Dorylus* under DORYLINAE. Add to MYRMICINAE: *Melissotarsus*; delete *Apterostigma*, *Myrmecocrypta*. Add to DOLICHODERINAE: *Turneria*; change *Dorymyrmex* to *Conomyrma*.

4. POGONOMYRMECOID—Delete from PONERINAE: *Myopopone*. Add to MYRMECIINAE: *Myrmecia*, *Nothomyrmecia*. Add to MYRMICINAE: *Adlerzia*, *Octostruma*, *Oxyopomyrmex*; delete *Novomessor*, *Basiceros*.

5. AMBLYOPONOID—Change last clause to “with or without minute teeth on medial surface.” Add to DORYLINAE: *Dorylus*. CERAPACHYINAE: change *Eusphinctus* to *Sphinctomyrmex*. Add to PONERINAE: *Myopopone*. Add to MYRMICINAE: *Apterostigma*, *Myrmicocrypta*, *Proatta*.

6. PRISTOMYRMECOID—MYRMICINAE: delete *Macromischoides*.

7. PHEIDOLOID—MYRMICINAE: add *Macromischa*, *Paedalgus*; delete *Melissotarsus*. Add *Aphomomyrmex* in FORMICINAE.

8. PLATYTHYREOID—Delete *Eubothroponera*.

11. DINOPONEROID—Delete “without a blade.” Add to PONERINAE: *Onychomyrmex*.

12. TETRAPONEROID—Add at end *Pseudomyrmex*.

14. RHYTIDOPONEROID—Change *Plagiolepis* to *Anoplolepis*.

16. TYPHLOMYRMECOID—Add *Apomyrma*.

A NEW SHAPE TYPE “19. OCHETOMYRMECOID—With a large (about $\frac{1}{3}$ total length) sharp-pointed apical tooth; with anterior and posterior subapical teeth, between which are numerous long needle-like teeth.” Occurrence.—MYRMICINAE: *Ochetomyrmex*. Add Fig. 2 to Fig. 20 in Memoir 7.

A NEW SHAPE TYPE “20. SIMOPONOID—Subtrapeziform; without a blade; masticatory border convex and bearing one apical and several medial teeth, which are sharp-pointed and of approximately the same size, and numerous small subapical teeth.” Occurrence: CERAPACHYINAE: *Simopone*. Add Fig. 3 to Fig. 20 in Memoir 7.

NAMES CHANGED

We have not attempted to note all name changes that have been made since our first article was published in 1928—but only those that might utterly confuse the modern user who has not kept up with synonymy.

Dorylinae

Eciton (*Acamatus*) is now genus *Neivamyrmex*.

Eciton (*Labidus*) is now genus *Labidus*.

Cerapachyinae

Change *Eusphinctus* to *Sphinctomyrmex*.

Ponerinae

1. Amblyoponini

Synonymize *Stigmatomma* under *Amblyopone*.

2. Platythyreini

Synonymize *Eubothroponera* under *Platythyrea*.

4. Ectatommini

Synonymize under *Heteroponera*: *Acanthoponera* (*Anacanthoponera*) and *Paranamopone*.

Synonymize under *Gnamptogenys*: *Holcoponera*, *Emeryella*, *Stictoponera*, *Ectatomma* (*Poneracantha*), *E. (Parectatomma)*, *E. (Gnamptogenys)*.

Synonymize *Chalcoponera* under *Rhytidoponera*.

7. Ponerini

Synonymize *Euponera* (*Trachymesopus*) under *Cryptopone*.

Myrmicinae

1. Myrmicini

Pogonomyrmex: raise *Ephebomyrmex* to a genus; delete (*Forelomyrmex*) *mayri*.

2. Pheidolini

Synonymize *Ischnomyrmex* under *Pheidole*.

Synonymize *Novomessor* under *Aphaenogaster*.

13. Leptothoracini

Change *Apsychomyrmex* to *Adelomyrmex*.

Change *Leptothorax canadensis* to *L. muscorum*.

18. Cryptocerini

Change to *Cephalotini*.

Dolichoderinae

Change *Dorymyrmex pyramicus* to *Conomyrma insana*.

Transfer *pruinosis* from *Iridomyrmex* to *Forelius*.

Formicinae

4. Formicini

Formica: delete (*Raptiformica*).

9. Plagiolepidini

Raise *Anoplolepis* to a genus.

10. Camponotini

Camponotus: raise (*Colobopsis*) to a genus.

SYSTEMATICS

Family Formicidae (pp. 45-66)

Replace our characterization of Formicidae (1st paragraph p. 46) with the following:

Soft, legless, translucent white (or whitish), with 13 somites. Thorax usually attenuated to form an obvious neck, but in many genera the head is applied to ventral surface without a neck. Leg, wing and gonopod vestiges present. Ten pairs of spiracles, one pair on each T2, T3, and AI-AVIII; peritremes of various widths and sclerotizations; atrial wall smooth or with minute spinules, which are isolated or in short rows; atrial walls of various thicknesses; atrial and tracheal openings of various ratios. Integument thin and delicate, with spinules usually present on some portion. Hairs usually abundant and moderately long; often branched or hooked. Head small but distinct (though not always conspicuous); not sclerotized and of same color as body. Eyes absent. Antennae one-segmented, usually reduced to mere discoids; usually with 3 sensilla each; high on cranium, mostly at or above middle half. Labrum a fleshy flap. Mandibles and pleurostomas the most sclerotized parts of the larva. Mandibles exceedingly varied in shape and sclerotization. Maxillae each with two one-segmented projections: palp and galea, the latter with two apical sensilla; lacinia indistinct. Labium lobose and usually with a transverse spinulose welt dorsally; bearing ventrally a pair of one-segmented palps; usually a sensillum between the palp and the opening of the sericteries; the latter a ventral transverse slit. Hypopharynx usually spinulose.

LARVAE OF THE SUBFAMILIES (pp. 46-66)

Revise DORYLINAE.—Profile myrmecoid. Leg vestiges conspicuous as slightly raised bosses. Antennae large, each with 2 sensilla. Clypeus and labrum not clearly distinguishable from each other. Mouth parts small and with few or no spinules. Mandibles amblyoponoid or dolichoderoid (*Cheliomyrmex*).

CERAPACHYINAE—Change last sentence to read: Mandibles amblyoponoid or simoponoid (*Simopone*).

MYRMECIINAE—In the last sentence change ectatommoid to pogonomyrmecoid.

PONERINAE—1. AMBLYOPONINI: In the first line delete *Amblyopone*, *Stigmatomma*; insert *Mystrium*; in the last line change *Stigmatomma* to *Amblyopone*; change *Onychomyrmex* to dinoponeroid. 7. PONERINI: Add at the end "pogonomyrmecoid (*Centromyrmex*)."

PSEUDOMYRMECINAE—In the last sentence insert *Pseudomyrmex* in the first parenthesis; add at the end "or platythyreoid (*Pseudomyrmex*) or dinoponeroid (*Pseudomyrmex*)."

MYRMICINAE—2. Revise: PHEIDOLINI—Profile aphaenogastroid (*Aphaenogaster*, *Oxyopomyrmex*, *Stenamma*, *Veromessor*) or myrmecoid (*Adlerzia*) or pogonomyrmecoid (*Goniomma*) or pheidoloid (*Machomyrma*, *Pheidole*). Maxil-

lary palp shorter than galea. Mandibles pogonomymecoid (*Aphaenogaster*, *Machomyrma*, *Oxyopomyrmex*, *Stenamma*, *Veromessor*) or pheidoloid (*Pheidole*) or ectatommoid (*Goniomma*). 3. MELISSOTARSINI—Substitute for phrase in brackets “(*Rhopalomastix*) or dolichoderoid (*Melissotarsus*).” Delete “proximal tooth very stout.” Add to profiles “or attoid (*Nothidris*).” 10. PHEIDOLOGE-TINI—Change to read “Profile pheidoloid or leptanilloid (*Trigonogaster*) or paedalgoid (*Oligomyrmex*, *Paedalgus*).” 11. MYRMECININI—Add to profile “except leptanilloid (*Dilobocondyla*).” Add at end “*Lordomyrma*, *Myrmecina*, *Terataner*.” 15. TETRAMORIINI—Add to second sentence “except *Eutetramorium*.” 16. OCHETOMYRMECINI—Substitute for the bracketed phrase “(*Wasmannia*) or ochetomyrmecoid (*Ochetomyrmex*).” 18. Change CRYPTOCERINI to CEPHALOTINI and delete last clause. 19. BASICEROTINI—Add *Octostruma* to pogonomymecoid profile. Change last sentence to read: Mandibles pogonomymecoid (*Aspididris*, *Octostruma*) or ectammoid (*Basiceros*, *Eurhopalothrix*, *Rhopalothrix*). 20. DACETINI—Revise: Profile pogonomymecoid (*Clarkistruma*, *Daceton*, *Orectognathus*) or aphaenogastroid (*Acanthognathus*, *Alistruma*, *Basiceros*, *Colobostruma*, *Epopostruma*, *Mesostruma*) or pheidoloid (*Smithistruma*, *Strumigenys*). Mandibles pogonomymecoid (*Alistruma*, *Epopostruma*, *Smithistruma*), ectatommoid (*Acanthognathus*, *Basiceros*, *Clarkistruma*, *Colobostruma*, *Mesostruma*, *Orectognathus*, *Strumigenys*), or dinoponeroid (*Daceton*). 24. PROATTINI—[Delete not studied]. Profile attoid but only slightly curved. Body and head hairs sparse, generally distributed. Mandibles amblyoponoid. 25. ATTINI—Change in parenthesis to read “except amblyoponoid (*Apterostigma*, *Myrmicocrypta*).”

DOLICHODERINAE—Delete from the first line “pheidoloid (*Engramma*).” FORMICINAE—Line 3. Add *Acantholepis* to oecophylloid profile and insert “ectatommoid (*Proformica*).” Line 6. Change *Plagiolepis* to *Anoplolepis*. 4. FORMICINI—Add at end “except ectatommoid in *Proformica*.” 6. GIGANTIOPI-NI—Line 4: delete “smooth.” 9. PLAGIOLEPIDINI—Revise: Profile pogonomymecoid (*Anoplolepis*) or oecophylloid (*Acantholepis*). Praesaepium, uncinate hairs and chiloscleres lacking. Mandibles rhytidoponeroid (*Anoplolepis*) or camponotoid (*Acantholepis*). 10. BRACHYMYRMECINI—Add *Aphomyrmex* and *Petalomyrmex* to pheidoloid profile; add another profile: dolichoderoid (*Paratrechina*). 12. CAMPONOTINI—Add to fourth sentence “(except sparsely in *Colobopsis*).”

KEY TO THE MATURE ANT LARVAE IN OUR COLLECTION

Add to last line on p. 71 *Oxyepoecus* and delete *Simopelta*. Delete from first line on p. 72 *Basiceros* and *Hylomyrma*.

Fit added genera into key (pp. 72–77):

Profile 1. Pogonomymecoid

- 11a. Labrum very broad (breadth 3 times length); genae bulging
..... *Dilobocondyla* in Myrmecini
- 11b. Labrum very broad (breadth 3 times length); genae not bulging
..... *Terataner* in Myrmecini
- 11c. Like neither of the above
Myrmica in Myrmicini, *Leptothorax* (*Mychothorax* and *Nesomyrmex*) in
Leptothoracini

- 13a. Head without hairs; body hairs long (0.05–0.2 mm), abundant and uniformly distributed *Amblyopone* in PONERINAE
- 13b. Head without hairs; body hairs short (0.03–0.1 mm), moderately numerous, except sparse on venter of abdomen *Mystrium* in PONERINAE
- 13c. Head without hairs; body hairs minute (0.013–0.06 mm) *Eutetramorium* in Tetramoriini
- 13d. Head with hairs 14
- 14f. Four hairs on dorsum of each T2, T3, AI-AV long and flexuous, with fan-shaped tip *Hylomyrma* in Myrmicini
- 14g. Body hairs of 2 types: (1) bifid to multifid, with short, straight-branched tip and (2) deeply bifid, with curled branches *Lordomyrma* in Myrmecini
- 14h. Two long uncinat hairs on dorsum of each AI-AVI, other body hairs short and denticulate *Octostruma* in Basicerotini
- 15a. Add: *Proformica* in FORMICINAE
- 15c. Each antenna minute and mounted on a teardrop-shaped base *Goniomma* in Pheidolini
- 17b. Neck long and slender, abdomen subovoidal but with ventral profile straight (all in PONERINAE from 17b through 25b) 19
- 19a. With 2–4 glabrous discoids on dorsum; typical tubercles consisting of a frustum surmounted by a spire, which is tipped with a spine-like hair *Anochetus* and *Odontomachus*
- 19b. With 2–4 glabrous discoids on dorsum; without such tubercles *Pachycondyla*
- 19c. With 2 unpaired doorknobs on dorsum *Myopias*
- 19d. With neither discoids nor doorknobs on dorsum 20
- 23c. Add *Plectroctena*
- 27a. Chiloscleres present (Tribe Camponotini) 28
- 27b. Chiloscleres lacking Tribes Formicini, Gesomyrmecini, Gigantiopini, Melophorini and Plagiolepidini
- 28a. Body hairs sparse, with a few very long whip-like hairs but without uncinat hairs *Colobopsis*
- 28b. Body hairs numerous, without long whip-like hairs but usually with a few uncinat hairs *Camponotus*, *Calomyrmex*, *Dendromyrmex*, *Echinopla*, *Opisthopsis*, *Polyrhachis*

Profile 2. Pheidoloid

- 1a. [Delete and substitute] Mandibles ochetomyrmecoid *Ochetomyrmex* in Ochetomyrmecini
- 2c. Body hairs mostly 2–3-branched; maxillae and labium with conspicuous conoidal projections *Petalomyrmex* in FORMICINAE
- 2d. Body hairs unbranched, smooth, the tip either long and flexuous or frayed *Aphomomyrmex* in FORMICINAE
- 9a. (Add *Vollenhovia* in Solenopsidini)

Profile 3. Dolichoderoid

- 1a. Mandibles amblyoponoid; body hairs numerous, branched, generally distributed *Paratrechina* in FORMICINAE
- 1b. Mandibles camponotoid; body hairs sparse, absent on sides; of 2 types: (1) short, fine and slightly curved; (2) long, stout, sinuate, uncinata, on dorsum *Azteca* in DOLICHODERINAE
- 1c. Mandibles dolichoderoid *DOLICHODERINAE 2
- 2a. Body without bosses *Dolichoderus*
- 2b. Body with bosses 3
- 3a. Bosses on dorsum only *Forelius*, *Froggattella* and *Iridomyrmex*
- 3b. Bosses ventral on thorax *Bothriomyrmex*
- 3c. With a pair of low bosses on prothorax and a single terminal boss ... *Engramma*
- 3d. With 2 dorsal bosses; tip of abdomen narrowed abruptly as a ventral tail *Turneria*
- 3e. Boss at or near posterior end of body 4
- 4a. Boss a conoidal projection just dorsal to anus *Conomyrma*
- 4b. Boss a posterodorsal knob or low swelling *Tapinoma*

Profile 4. Attoid

- 1c. Mandibles ectatommoid *Nothidris* in Solenopsidini
- 1d. Mandibles amblyoponoid *Proatta* in Proattini

Profile 5. Myrmecioid

- 1a. Mandibles simoponoid *Simopone* in CERAPACHYINAE
- 1b. Mandibles pogonomyrmecoid 6
- 1c. Mandibles diacammoid *Megaponera* in PONERINAE
- 1d. Mandibles dolichoderoid *Cheliomyrmex* in DORYLINAE
- 1e. Mandibles amblyoponoid 2
- 1f. Mandibles ectatommoid *Myopopone* in PONERINAE
- 2a. Maxillary palp bootee-shaped *Prionopelta* in PONERINAE
- 2b. Maxillary palp not bootee-shaped 3
- 3a. Maxillary and labial palps represented by 7–15 scattered sensilla *Dorylus* in DORYLINAE
- 3b. Maxillary palp a conspicuous compact group of sensilla which is more or less elevated *Eciton* in DORYLINAE
- 3c. Maxillary palp different from the above 4
- 4a. With a row of long uncinata hairs around each somite *Lioponera* in CERAPACHYINAE
- 4b. Not as above 5
- 5a. Head hairs moderately numerous (50–100) *Aenictus*, *Labidus* and *Neivamyrmex* in DORLYINAE
- 5b. Head hairs few (10–25) *Cerapachys*, *Phyracaces* and *Sphinctomyrmex* in CERAPACHYINAE
- 6a. Body hairs sparse; antennae minute; mandibles with a single medial tooth *Adlerzia* in Pheidolini

- 6b. Body hairs numerous; antennae moderately large; mandible with 2 medial teeth MYRMECIINAE

Profile 7. Aphaenogastroid

- 1c. Mandibles ectatommoid
 *Ocymyrmex* in Ocymyrmecini, *Basiceros* in Basicerotini and
 *Acanthognathus* in Dacetini
 2e. Some body hairs uncinat *Rhopalothrix* in Basicerotini
 2f. Body hairs few, short, with frayed tip (some bent)
 *Oxyopomyrmex* in Pheidolini

Profile 11. Oecophylloid

Delete *Oecophylla* after characterization.

- 1a. Posterior half of abdomen conspicuously tapered; body hairs whip-like or denticulate, long (0.025–0.075 mm) ... *Acantholepis* in FORMICINAE
 1b. Posterior half of abdomen not tapered; body hairs simple and very short (0.006–0.036 mm) *Oecophylla* in FORMICINAE

Profile 12. Rhopalomastigoid

Delete *Rhopalomastix* after characterization.

- 1a. Mandibles pogonomyrmecoid *Rhopalomastix* in Melissotarsini
 1b. Mandibles dolichoderoid *Melissotarsus* in Melissotarsini

DIFFERENCES IN SEX AND CASTE (p. 78)

D. Wheeler and Nijhout (1981) found that *Pheidole bicarinata* soldier larvae have prominent mesothoracic wing discs; these are suppressed in minor worker larvae.

INTERNAL ANATOMY (p. 80)

Add to end of paragraph 2: We have at last prepared our own diagram of the internal anatomy of a hymenopterous larva. See 1979:320.

LIFE CYCLE (p. 80–82)

Substitute the following for the first two sentences in the last paragraph on p. 80: One source of confusion lies in the inclusion or exclusion of the prepupa (= semipupa). This is actually the pharate stage of the pupa. Nevertheless the integument in which the pupa develops is that of the last larval instar, although the body-shape may change: the thorax usually thickens and the body becomes straighter. There must be an ecdysis in which the fully formed pupa casts off that last larval integument.

Substitute for the fourth complete paragraph on p. 81: Onoyama (1982) has prepared a table of known numbers of instars reported in the literature together with characters used and references. We repeat here his table in a modified form and bring it up to date.

COCOONS (p. 82)

Add the 2 following paragraphs under WEAVING on p. 82.

Hölldobler and Wilson (1983) have recounted in detail the behavior of workers

Table 1. Larval instars in ants.

Ant	Instars	Characters Used	Our Reference
<i>Acantholepis frauenfeldi</i>	5	larval shape and size, chaetotaxy	1982
<i>Acromyrmex octospinosus</i>	4	length, hair, diameter of spiracle	
<i>Aphaenogaster rudis</i>	5	hair distribution, shape and length	1953
<i>Brachyponera chinensis</i>	4	head width	
<i>Cataglyphis cursor</i>	3	size, diameter of T2 spiracle, hairs, head, mouth parts	
<i>Crematogaster stadelmanni</i>	3	mandible size, chaetotaxy	1976
<i>Crematogaster striatula</i>	3	chaetotaxy, diameter of spiracle	1983
<i>Formica japonica</i>	3	head length	
<i>Messor aciculatus</i>	3	chaetotaxy	
<i>Myrmica rubra</i>	3	hair density	1976
<i>Myrmica ruginodis</i>	3	hair density, maxillary palp and galea	1983
<i>Pheidole bicarinata</i>	4	hair pattern, mandible, spiracle size	
<i>Pheidole pallidula</i>	4	spiracle size, hair shape, mandible	
<i>Plagiolepis pygmaea</i>	5	body shape, chaetotaxy	1974
<i>Polyrhachis lamellidens</i>	4	head width, hair shape	
<i>Solenopsis invicta</i>	4	mouth parts	1983
<i>Tetramorium caespitum</i>	3	hair shape	
<i>Tetramorium caespitum</i>	3	head width, mandible, maxilla, chaetotaxy	

and larvae during the weaving process in the three genera mentioned above and also in the neotropical genus *Dendromyrmex*. The small colonies of *Dendromyrmex* “build oblong carton nests on the leaves of a variety of tree species in the rain forest.” The carton is “reinforced with continuous sheets of larval silk.” These authors doubt (p. 491) that the larvae of *Technomyrmex bicolor textor* Forel produce silk used in the construction of nests.

CARE (p. 85)

Insert as the last paragraph under FEEDING:

An excellent general account of feeding is to be found in Wheeler and Bailey 1920:250–275.

A new topic to be added at the end of BIONOMICS (p. 85):

MIMICRY

Cross (1965:61) stated that “The physogastric females (figs. 8, 9) of [the mite genus *Perperipes* (Pyemotidae)] differ greatly from all other pyemotids, and apparently are mimics of the doryline ant larvae among which they live.” (See also Audy et al., 1972:490.)

TAXONOMIC CONCLUSIONS (pp. 88–93)

On page 89 we listed the myrmecological uses for the study of ant larvae. We now list 2 more:

4. Distinguish instars. We regard the mature worker larva as the definitive representative of a genus or species, but we have described younger stages whenever they were available. We have rarely, however, been sure of the instars. For such determination we should have an egg ready to hatch and a larva of each instar ready to molt; in each case the next stage will be fully formed inside and, by our technique, we can see both at once. We also need the semipupa, which will show all characters of the mature larva except shape. Because such critical specimens are rarely found it behooves the collector to get as much brood as possible. But who is interested in instars? Since caste is determined in the larval stage, all biologists would like to know when and how, and someday the applied entomologist may *need* to know.

5. As an aid in taxonomy. We have always believed that ant taxonomy should be based on both larval and adult characters. Larval characters can be particularly useful when adult characters are indistinct.

LARVAL CLASSIFICATION VS. ADULT CLASSIFICATION (pp. 92–93)

Larval classification supports the following changes since the "Genera Insectorum" (1910–1925):

5. Brown (1975:4) uses our study of the larvae to support his synonymizing *Eubothroponera* into *Platythyrea*.

6. Urbani (1977:428) states that larval characters were the best justification for the separation of the Leptanillinae from the Dorylinae. ("L'elevazione a sottofamiglia dell'antica tribù *Leptanillini* è dovuta a G. C. ed E. W. Wheeler (1930), ma la migliore giustificazione di questo punto di vista la si trova nel lavoro di G. C. e J. Wheeler (1965) dove vengono accuratamente studiate le morfologie larvali delle tre specie di cui si conoscono anche gli stadi preimaginali.")

Larval classification does not support the following changes:

4. Dorylinae. The splitting of this subfamily into Old World and New World subfamilies. We have discussed this at length in our 1984 and 1985.

5. Ponerinae. Brown's 1976 reduction of the tribe Odontomichini to a subtribe. See our 1985:260.

IMPORTANCE OF LARVAE

(p. 93, add after "Taxonomic Conclusions")

We cannot give this topic the space it deserves; furthermore it is outside the main field of our research. Nevertheless it must be discussed in any comprehensive treatment of ant larvae. Fortunately Abbott (1978:236, 242–243) has given a complete and documented survey. Shorter treatments: Febvay and Kermarrec, 1981; Hunt, 1982; Peacock et al., 1950; Schneirla, 1971:141–142; Wheeler and Wheeler, 1979a:334–336; Wüst, 1973:417. For a thumbnail sketch we have found nothing better than one sentence in a 1978 review by S. C. Stearns in the *American Scientist* 66:623: "Adults ants are dependent on soluble proteins and amino acids received from the larvae, which digest protein for the whole colony."

As a finale we quote the last paragraph in our 1979 chapter on *Larvae of Social Hymenoptera*: "This brings us back again to the idea of the colony as a superorganism. The crops of all adult members of a colony have been referred to as the collective stomach of a colony. Now we have to add the larvae of ants and wasps as a sort of collective digestive gland necessary for the health of the colony."

THE FUTURE
(add after "Importance of Larvae")

Our stream of incoming larvae has dwindled to a mere trickle. Our supply from Australia has been hampered by governmental export regulations. Our American colleagues who supplied the most larvae have reduced their field activities—as have we. Our lament was well expressed by Dr. W. L. Brown years ago: "If only I could get myrmecologists to collect larvae!" So we ask our young colleagues to collect and send us larvae.

Recently we were commenting to a young colleague (who is sending us larvae) that we were not getting larvae of new genera. He retorted: "The genera you have not studied are those whose nests are found only by accident." That had not occurred to us. We know that many nests have no superstructure around the entrance, which is just a hole in the ground; some genera nest in leaf mold or duff, others in plant cavities.

So we looked up the history of 103 genera which we have not studied: 62% have been reported only once (probably the type nest or only the type specimen), 23% we consider rare, and only 15% common.

In view of the above we have the following observations to make concerning the future of the study of ant larvae. The remaining common genera will be described. Some of the "only once" and the rare will be accidentally found and described, but some will never be discovered; they may be extinct already as the result of the degradation of the habitat. The younger stages of most genera will be needed in order that instars may be identifiable. We have studied ant larvae at the generic level. There will doubtless be problems where intraspecific and interspecific differences must be studied. Investigators must also be aware of the intranidal differences. The anatomy and function of protuberances, chiloscleres and unnamed structures will be studied. Because of the importance of larvae to the well-being of the colony, the physiology and behavior of the colony with reference to the larvae must be learned. Ant larvae will play a larger role in systematics. Where adult taxonomy is dubious, larval similarities or differences will be an aid in taxonomy.

A. TAXONOMIC BIBLIOGRAPHY OF OUR PUBLICATIONS ON ANT LARVAE
(pp. 93–96) [ADDITIONS ONLY]

General

- 1976. Ant Larvae: Review and Synthesis. Entomol. Soc. Wash., Mem. No. 7. 108 pp.
- 1979a. Larvae of the social Hymenoptera. Chap. 7, pp. 287–338. *In* Social Insects. Vol. I. H. R. Hermann, ed. Academic Press, New York.
- 1979b. Larvae of some eusocial bees and wasps. Nat. Hist. Mus. Los Ang. Cty. Mus. Contrib. Sci. No. 321, 19 pp.
- 1985. A simplified conspectus of the Formicidae. Trans. Am. Entomol. Soc. 111: 255–264.

Dorylinae

- 1984. The larvae of the army ants: a revision. J. Kans. Entomol. Soc. 56: 263–275.

Ceropachyinae

- 1974a. Supplementary studies on ant larvae: *Simopone* and *Turneria*. J. N.Y. Entomol. Soc. 82: 103–105.

Myrmeciinae

- 1980a. Larval and egg stages of the primitive ant *Nothomyrmecia macrops* Clark. J. Aust. Entomol. Soc. 19: 131–137 (with R. W. Taylor).

Ponerinae

- 1976b. Supplementary studies on ant larvae: Ponerinae. Trans. Am. Entomol. Soc. 102: 41–64.
1980b. Supplementary studies on ant larvae: Ponerinae, Myrmicinae and Formicinae. Trans. Am. Entomol. Soc. 106: 527–545.
1985b. The larvae of *Dinoponera*. Psyche 92: 387–391.
1986a. Supplementary studies on ant larvae: Ponerinae. Trans. Am. Entomol. Soc. 112: 85–94.

Myrmicinae

1977. Supplementary studies on ant larvae: Myrmicinae. Trans. Am. Entomol. Soc. 103: 581–602 [Tribes: Myrmicini, Pheidolini, Cardiocondyliini, Solenopsidini, Pheidologetini, Myrmecini, Leptothoracini, Ochetomyrmecini, Basicerotini, Attini].
1980b. See above under Ponerinae. [Tribes: Melissotarsini, Solenopsidini, Myrmecini, Tetramoriini, Basicerotini.]
1983. Supplementary studies on ant larvae: Myrmecinae. Trans. Am. Entomol. Soc. 108: 601–610 [Tribes: Myrmicini, Pheidolini, Solenopsidini, Myrmecini, Meranoplini, Cephalotini, Basicerotini, Attini].
1986b. Supplementary studies on ant larvae: Myrmicinae. J. N. Y. Entomol. Soc. (in press) [Tribes: Myrmicini, Pheidolini, Crematogastrini, Pheidologetini, Leptothoracini, Tetramoriini, Cephalotini, Basicerotini, Dacetini, Attini].
1985c. The larva of *Proatta*. Psyche 92: 447–450 [Tribe: Proattini].

Dolichoderinae

- 1974a. See above under Ceropachyinae.

Formicinae

- 1974b. Supplementary studies on ant larvae: *Teratomyrmex*. Psyche 81: 38–41.
1980b. See above under Ponerinae.
1982. Supplementary studies on ant larvae: Formicinae. Psyche 89: 175–181.
1986c. Supplementary studies on ant larvae: Formicinae. J. N. Y. Entomol. Soc. 94: 331–341.

B. MATERIAL STUDIED (pp. 96–101)

(Changes in our collection since 1976; all are additions unless otherwise indicated.)

Dorylinae

Aenictus: change *martini* to *gracilis* Emery; change *turneri* to *ceylonicus* (Mayr). *Dorylus* (*Anomma*): *molesta* Gerstäcker; (*Alaopone*) sp.; (*Dorylus*) sp.; (*Rhogmus*) sp.

Neivamyrmex: *harrisi* (Haldeman), *opacithorax* (Emery), *postcarinatus* Borgmeier, *texanus* Watkins.

Cerapachyinae

Simopone: *conciliatrix* Brown.

Myrmeciinae

Nothomyrmecia: *macrops* Clark.

Ponerinae

1. Amblyoponini. *Mystrium*: *mysticum* Roger. 2. Platythyreini. Delete *Eutbothroponera tasmaniensis*. *Platythyrea*: *modesta* Forel, *parallela* (F. Smith), *pilosula* (F. Smith), *tasmaniensis* (Forel), *turneri* Forel; delete *australis*, *incerta*. 3. Typhlomyrmecini. *Typhlomyrmex*: *rogenhoferi* Mayr. 4. Ectatommini. *Gnampotogenys*: *binghami* (Forel), *costata* Emery. *Heteroponera*: *dolo* (Roger). 6. Proceratiini. *Proceratium*: unidentified sp. = *avium* Brown. 7. Ponerini. *Bothroponera*: *tessierinodis* (Emery), *tridentata* F. Smith. *Brachyponera*: *luteipes* (Mayr). *Centromyrmex*: *bequaerti* Emery. *Dinoponera*: *gigantea* (Perty); change *grandis* to *mutica* Emery. *Leptogenys*: *aspersa* Ern. André, *diminuta* (F. Smith), *iridescens* (F. Smith), *kitteli* Mayr. *Mesoponera*: *ferruginea* (F. Smith). *Plectroctena*: *cryptica* Bolton, *Myopias*: *cribriceps* Emery. 8. Odontomachini. *Anochetus*: *inermis* Ern. André, *gladiator* Mayr, *princeps* Emery, *rugosus* (F. Smith), *testaceus* Forel. *Odontomachus*: *biumbonatus* Brown, *erythrocephalus* Emery, *insularis* Guérin, *simillimus* F. Smith, *tyrannicus* F. Smith, sp.; change *haematoda* to *haematodus*.

Myrmicinae

1. Myrmicini. *Hylomyrma*: *reitteri* (Mayr), sp. = *versuta* Kempf. *Manica* sp. = *yessensis* Azuma. 2. Pheidolini. *Adlerzia*: *froggatti* Forel. *Aphaenogaster*: (*Atto-myрма*) sp., (*Deromyrma*) *swammerdami* Forel. *Goniomma*: *hispanicum* (Ern. André). *Oxyopomyrmex*: sp. Make *Novomessor* a subgenus of *Aphaenogaster*. Delete *Ischnomyrmex*. Add *longiceps* (F. Smith) to *Pheidole*. 3. Melissotarsini. *Melissotarsus*: *titubans* Delage. 9. Solenopsidini. *Antichthonidris*: *bidentatus* (Mayr), *denticulatus* (Mayr). *Liomyrmex*: sp. *Nothidris*: *latastei* (Emery). *Oxyepoecus*: *punctifrons* (Borgmeier), *rastratus* (Mayr); delete "one unidentified species." *Solenopsis*: *invicta* Buren, *richteri* Forel. *Vollenhovia*: sp., sp. 10. Pheidologetini. *Paedalgus*: sp. 11. Myrmecini. *Lordomyrma*: sp. *Terataner*: *alluaudi* (Emery). 12. Meranoplini. *Calyptomyrmex*: *nummuliticus* Santschi. 15. Tetramoriini. *Eutetramorium*: *mocquerysi* Emery. 16. Ochetomyrmecini. *Ochetomyrmex*: *subpolitus* Wheeler. 18. Change Cryptocerini to Cephalotini. *Cephalotes*: *alfaroi* (Emery). 19. Basicerotini. *Basiceros*: *manni* Brown and Kempf, *singularis* (F. Smith), sp. *Octostrumma*: *inca* Brown and Kempf. 24. Proattini. *Proatta* *butteli* Forel. 25. Attini. *Cyphomyrmex*: *hamulatus* Weber.

Dolichoderinae

3. Tapinomini. *Turneria: dahli* Forel.

Formicinae

4. Formicini. *Cataglyphis: bicolor* (Fabricius). *Proformica: ferrerii* Bondroit. *Teratomyrmex: greavesi* McAreavey. 9. Plagiolepidini. *Acantholepis: capensis* Mayr. *Acropyga: sp.* 10. Brachymyrmecini. *Aphomomyrmex: afer* Emery. *Brachymyrmex: admotus* Mayr, *giardi* Emery. *Paratrechina: guatemalensis* (Forel), *longicornis* (Latreille), *wojciki* Trager. *Petalomyrmex phylax* Snelling. 12. Camponotini. *Dendromyrmex: chartifex* (F. Smith).

C. ENEMIES OF ANT LARVAE (p. 102) [ADDITIONS]

Phylum Sporozoa

- Burenella dimorpha*. Parasite. *Solenopsis geminata*.

Phylum Platyhelminthes

- Anomotaenia brevis* larva. Parasite. *Leptothorax nylanderii*.

Phylum Nematoda

- Add *Pheidole* to list of hosts.

Phylum Arthropoda

Class Insecta

Order Coleoptera

- HISTERIDAE: *Euxenister caroli*. Predation. *Eciton burchelli*. *Euxenister wheeleri*. Predation. *Eciton hamatum*. *Pulvinister nevermanni*. Predation. *Eciton hamatum*.

- PSELAPHIDAE: *Adranes taylori*. Fed by ant larvae by trophallaxis. *Lasius sitkaenesis*.

Order Lepidoptera

- LYCAENIDAE: Add to prey *Myrmica*, *Oecophylla*, *Tetramorium*, *Tapinoma*. Add to predators *Liphyra brassiolis*, *Maculinea alcon*, and *M. arion*.

- PYRALIDIDAE: *Wurthia aurivillii* and *W. myrmecophila*. Predation. *Oecophylla* and *Polyrhachis*.

- COSMOPTERYGIDAE: *Batrachedra*. Predation. *Polyrhachis dives*.

Order Diptera

- CHIRONOMIDAE: *Forcipomyia*. Predation. *Formica*.

- SYRPHIDAE: *Microdon fuscipennis*. Predation. *Forelius pruinus*.

Order Neuroptera

- CHRYSOPTIDAE: *Italochrysa*. Predation. *Crematogaster*.

Order Hymenoptera

- EUCHARITIDAE: *Orasema crassa*, *Orasema* sp. Parasitoid. *Solenopsis invicta*.

Class Arachnida
Order Acarina

Parasitid mites. Parasitic. New World army ants.

E. SPECIALIZATION INDICES—CHANGES AND ADDITIONS (p. 104)

SUBFAMILY DORYLINAЕ 26: *Aenictus* 24, *Cheliomyrmex* 27, *Dorylus* 30, *Eciton* 24, *Labidus* 22, *Neivamyrmex* 29.

SUBFAMILY CERAPACHYINAЕ 22: *Simopone* 24.

SUBFAMILY MYRMECIINAЕ 24: *Myrmecia* 24, *Nothomyrmecia* 24.

SUBFAMILY PONERINAЕ: TRIBE AMBLYOPONINI: *Mystrium* 14; TRIBE PONERINI: *Plectroctena* 12.

SUBFAMILY MYRMECINAЕ: TRIBE MYRMICINI: *Hylomyrma* 15; TRIBE PHEIDOLINI: *Adlerzia* 14, *Goniomma* 17, *Oxyopomyrmex* 15; TRIBE MELIS-SOTARSINI 32: *Melissotarsus* 33; TRIBE SOLENOPSIDINI 21: *Antichthonidris* 14, *Nothidris* 26, *Oxyepocus* 15. TRIBE PHEIDOLOGETINI: *Paedalgus* 25. TRIBE MYRMECININI 20: *Lordomyrma* 16, *Terataner* 20. TRIBE TETRA-MORIINI 12: *Eutetramorium* 11. TRIBE OCHETOMYRMECINI: *Ochetomyr-mex* 18. TRIBE BASICEROTINI 15: *Octostruma* 9. TRIBE PROATTINI 25: *Proatta* 25.

SUBFAMILY DOLICHODERINAЕ: *Turneria* 27.

SUBFAMILY FORMICINAЕ: TRIBE FORMICINI: *Cataglyphis* 15, *Profor-mica* 18, *Teratomyrmex* 14. TRIBE PLAGIOLEPIDINI 14: *Acantholepis* 17. TRIBE BRACHYMYRMECINI: *Aphomomyrmex* 13, *Petalomyrmex* 22. TRIBE CAMPONOTINI: *Colobopsis* 19.

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THE REDISCOVERY AND SYSTEMATIC POSITION OF
ACOLHUA CHAMPIONI DISTANT (HEMIPTERA: LYGAEIDAE)

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Abstract.—*Acolhua championi* previously known from a single mutilated specimen is redescribed and figured from Oaxaca, Mexico. The genus *Acolhua* Distant is redescribed and transferred from the Drymini to the Antillocorini. The cladistic relationships are discussed.

Despite Distant's inclusion of a colored figure of *Acolhua championi* (Distant, 1893, pl. 34, fig. 24), the genus *Acolhua* has remained an enigma since its original description. Distant related it to *Clerada* but since the tribe Cleradini is restricted to the Eastern Hemisphere this has seemed highly improbable. Slater's (1964) Catalogue listed it in the Drymini. It has been known only from the holotype in the British Museum. This specimen as Scudder (1967) correctly notes lacks an abdomen. Since the position of the abdominal spiracles and the number and placement of the trichobothria, the presence or absence of inner laterotergites, the number of dorsal scent gland orifices, as well as details of the genitalia, are essential for assignment to a tribe, it has been impossible to place this genus accurately.

Recently we have been able to examine a series of five specimens of *A. championi* from Oaxaca, Mexico, collected by beating dry leaves of *Cecropia* sp. by E. Barrera. Examination of these specimens makes it possible to determine that *Acolhua* is a member of the Antillocorini and to discuss its cladistic position within this tribe.

This placement of *Acolhua* in the Antillocorini rather than the Drymini confirms Slater's (1986) belief that the tribe Drymini is not represented in the neotropical fauna whereas the Antillocorini constitute a diverse and abundant element there.

Slater (1980) discussed the systematic relationships of the Antillocorini of the Western Hemisphere and presented a preliminary generic cladogram. *Acolhua championi* appears to be most closely related cladistically to the genus *Paradema* Slater and within the genus to *Paradema englemanni* Slater. Both of these genera have the sperm reservoir and attendant wings reduced to a minute sclerite attached to the proximal end of the ejaculatory duct which in *Paradema englemanni* and *Acolhua championi* is enormously enlarged (see Slater, 1980, figures 16 and 17). These two species are also similar in being the only taxa with such a phallic configuration that have distinctly concave apical corial margins. Both species also

have the sutures between sterna 3–4 and 4–5 almost completely obliterated by the high degree of sternal fusion (Fig. 3); both have numerous elongate upstanding hairs on the dorsal surface of the body and on the antennae and have three distinct rows of claval punctures.

Despite these cladistically noteworthy similarities the two species have many differences that warrant the retention of *Acolhua* as a distinct genus. While both *A. championi* and *P. englemani* have black shining heads, that of *P. englemani* is declivent anteriorly and the eyes are not stalked. *Acolhua* has an almost completely polished shining dorsal and ventral surface, whereas *Paradema englemani* has the pronotum, scutellum, fore wings, propleuron, prosternum, mesopleuron and anterior lobes of the metapleuron pruinose. The metathoracic scent gland auricle of *P. englemani* is not short and rounded as it is in *A. championi* but angles almost straight caudo-laterally, and the evaporative area extends almost to the middle of the metapleuron.

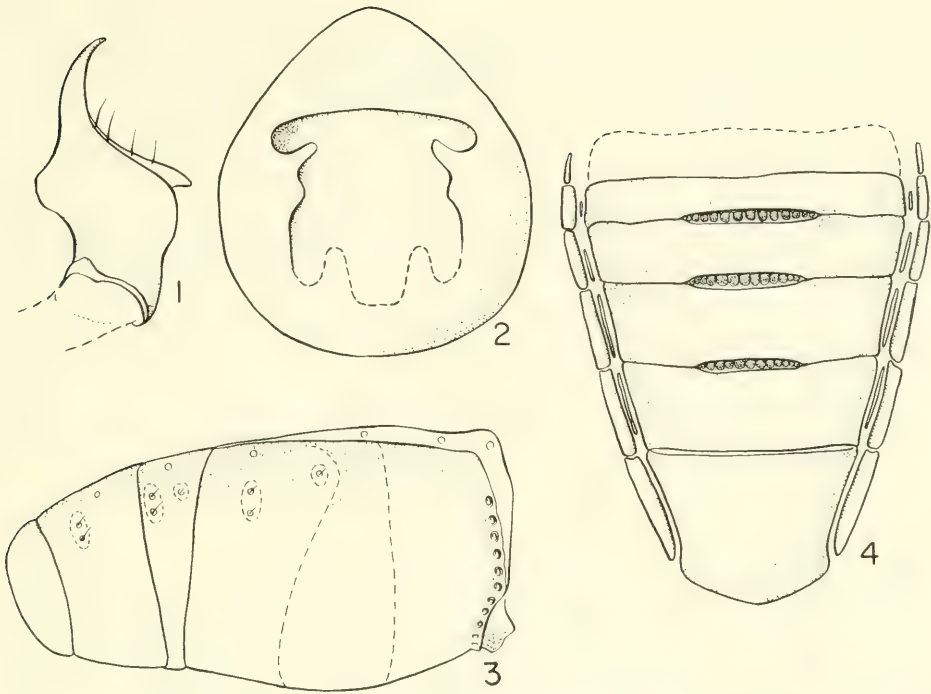
If Slater's (1980) cladogram is correct *Acolhua* is the sister group to *Paradema* and its sister species is *Paradema englemani*. This means that if present nomenclature is retained *Paradema* becomes paraphyletic. This paraphyly could be avoided by elevating *P. englemani* to generic status and as noted above there are synapomorphies that unite *P. englemani* and *Acolhua*. *Acolhua championi* has numerous striking autopomorphies. It is certainly worthy of generic status and except for the synapomorphies noted above is not closely related morphologically to *Paradema englemani*. We do not think it reasonable to combine *P. englemani* with *Acolhua* nor to remove *P. englemani* from *Paradema*. We believe that there is both practical and theoretical value in sometimes retaining paraphyletic taxa and that this is a good example.

All measurements are in millimeters.

Acolhua Distant

Acolhua Distant 1893 p. 394 (see colored figure).

Body above and below polished and shining. Clavus and posterior two-thirds of scutellum contrastingly pruinose. Head non-declivent. Eyes strongly protruding and placed on short but distinct stalks. Pronotum with a narrow anterior collar bounded posteriorly by a row of coarse punctures. Lateral pronotal margins rounded or very faintly calloused, not carinate or explanate. Transverse pronotal impression obsolete. Scutellum lacking a median elevation. Clavus with three distinct rows of punctures of similar size. Apical corial margin deeply concave mesally. Gular trough elongate, tapering to a blunt point posteriorly, extending to level of antenniferous tubercles. Metathoracic scent gland auricle short and rounded, slightly curved caudad. Evaporative area small, extending only slightly beyond auricle, outer margin rounded, covering only ventral one-third of metapleuron and remote from entire posterior margin. Fore femora slender, mutic. Abdomen with well developed equal-sized scent gland scars present between terga three and four, four and five, and five and six (Fig. 4). Inner laterotergites present on terga three through six (Fig. 4). Spiracles of abdominal segments three and four both lying ventrally on sternal shelf (Fig. 3). Anterior segments of abdominal sternum fused so that sutures between sterna three and four and four and five are invisible or at most represented by a very faint impression. Trichobothria of sternum five not linear,



Figs. 1–4. *Acolhua championi*. 1, Paramere. 2, Genital capsule (dorsal view). 3, Abdomen (lateral view). 4, Abdomen (dorsal view).

two posterior trichobothria located one above the other and almost directly below spiracle of segment five (Fig. 3). Sperm reservoir minute with tiny obsolete wings. Ejaculatory duct enormously wide for almost entire length. Paramere (Fig. 1) with short slender blade, broad posterior lobe, a short but acute inner lobe. Genital capsule as in Figure 2.

Type species.—*Acolhua championi* Distant. Monobasic.

Acolhua championi Distant

Acolhua championi Distant 1893, p. 394.

Head, anterior pronotal lobe, central area of posterior pronotal lobe, base of scutellum, meso- and metapleuron and sternum, first antennal segment, distal ends of second and third segments and extreme base of segment four black. Anterior pronotal collar from meson to laterad of ocelli yellow. Dark red brown as follows: lateral and posterior areas of pronotum, scutellum, clavus, posterior two-thirds of corium, abdomen and all femora (sometimes paler yellowish brown on pronotum and clavus). A white macula, formed by the two clavi, present along claval commissure. Basal area of corium to level of middle of clavus white or pale yellow. Membrane hyaline with dark brown streaks and mottled areas and a large white macula present adjacent to apex of corium.

Dorsal surface of body, legs, and antennae bearing numerous elongate upstanding hairs, those on antennae often two or more times as long as diameter of a

segment. Dorsal surface of head deeply rugulose. Pronotum, scutellum, clavus and anterior portion of corium bearing large coarse punctures. Calli smooth. Posterior two-thirds of corium convex and bearing only a few punctures adjacent to distal end of corial furrow.

Tylus attaining distal one-third of first antennal segment. Length head 0.52, width 0.70, interocular space 0.42. Lateral pronotal margins slightly impressed in area of obsolete transverse impression. Humeral angles of pronotum evenly rounded. Posterior pronotal margin evenly convex. Length pronotum 0.58, width 1.0. Length scutellum 0.50, width 0.56. Length claval commissure 0.26. Midline distance apex clavus-apex corium 0.50. Midline distance apex corium-apex membrane 0.40. Length labial segments I 0.28, II 0.26, III 0.26, IV 0.16. Antennal segments one, two and three slender, terete, segment four robustly fusiform. Length antennal segments I 0.24, II 0.46, III 0.36, IV 0.44. Total body length 2.72.

Material examined.—5 males MEXICO: *Oaxaca*, Pluma Hidalgo 1070 S.N.M., 3.VI.1985 (E. Barrera). In Instituto de Biología UNAM, Mexico D. F. and J. A. Slater collections.

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SURVEY OF THE NUMBER OF OVARIOLES IN VARIOUS TAXA OF BEES (HYMENOPTERA: APOIDEA)

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Abstract.—The numbers of ovarioles in 15 taxa of bees are reported for the first time and compared with published accounts for other taxa of bees (Iwata, 1955, 1965; Iwata and Sakagami, 1966).

Ronald J. McGinley and I recently undertook a study of the nesting biology, immature stages, and adult anatomy of the Palearctic bee *Pararhophites orobinus* (Morowitz) in an attempt to determine the taxonomic and phylogenetic relationships of this genus to other long-tongued bees. In the process I compared the ovaries of female specimens preserved in Kahles solution at the American Museum of Natural History with those of various taxa of bees as reported by Iwata (1955, 1965) and Iwata and Sakagami (1966). Although my material did not permit a detailed analysis of oocyte shape and size, it did show that *Pararhophites orobinus* possesses only three ovarioles in each of its two ovaries (i.e. 3:3). Michener (1944), Michener and Moure (1957), and Popov (1949) had all considered *Pararhophites* to be an anthophorid. Iwata and Sakagami (1966) pointed out that the Anthophoridae, as well as the Apidae, normally have four ovarioles in each ovary (i.e. 4:4), although parasitic and social forms of these two families usually have a larger number of ovarioles. Colletidae, Andrenidae, Halictidae and Megachilidae, on the other hand, have three ovarioles per ovary (3:3). After examining *Pararhophites*, I dissected specimens of various taxa of bees (many of them of special systematic interest in my past studies) preserved in Kahles to determine whether the ovaries of other taxa correspond to the published information. Although specimens were few, variation in numbers of ovarioles within a taxon is normally quite limited, so that the numbers given in Table 1 are probably reliable. This paper also offers a few observations and conclusions, in addition to the figures in Table 1.

In general, the number of ovarioles in an ovary (Table 1) corresponded to the account by Iwata and Sakagami (1966). The Melittidae (*Macropis* and *Megano-mia*), like other short-tongued bees, also have a 3:3 formula. The Fidelinae (*Fidelia*), considered by me as a primitive offshoot of the Megachilidae, have a 3:3 formula, as do the other megachilids. The parasitic anthophorines of the Nomadinae (*Kelita* and *Oreopasites*) exhibited a formula of at least 5:5 (and have small oocytes) that corresponds to the large number of ovarioles found in the nomadines *Nomada* and *Epeolus*, as reported by Iwata (1955) and Iwata and Sakagami (1966).

Table 1. Number of ovarioles in various taxa of bees.

Taxon	Number of Specimens Examined	Number of Ovarioles
Colletidae		
Diphaglossinae		
<i>Ptiloglossa arizonensis</i>	2	3:3
Andrenidae		
Andreninae		
<i>Megandrena mentzeliae</i>	1	3:2 ^a
	1	3:3
Panurginae		
<i>Cephalurgus anomalis</i>	2	3:3
<i>Meliturgula minima</i>	2	3:3
<i>Nomadopsis barbata</i>	2	3:3
<i>Panurgus intermedius</i>	10	3:3
<i>Perdita</i> n. sp. nr. <i>wootonae</i>	2	3:3
<i>P. portalis</i>	2	3:3
Melittidae		
Meganomiinae		
<i>Meganomia gigas</i>	2	3:3
Melittinae		
<i>Macropis nuda</i>	2	3:3
Megachilidae		
Fideliinae		
<i>Fidelia villosa</i>	2	3:3
Anthophoridae		
Nomadinae		
<i>Kelita chilensis</i>	1	prob. 5:5
<i>Oreopasites vanduzeei</i> ^b	1	approx. 11 total
	1	prob. 5:5
Anthophorinae		
<i>Exomalopsis solidaginis</i>	5	4:4
<i>Pararhophites orobinus</i>	2	3:3

^a Although one ovary seemed to have only two ovarioles, I assume that one was obscured but actually present.

^b Many ovarioles were present in this species. Because at least 11 could be counted in one specimen, I assumed it had an actual count of either 5:5 or 6:6. The other specimen appeared to have 5:5.

The family placement of *Pararhophites*, considered a "primitive" anthophorid by Michener and Moure (1957) and Popov (1949), is suspect because *P. orobinus* has only three ovarioles in each ovary. Such a feature may be plesiomorphic and, therefore, not inconsistent with placing the genus in the Anthophoridae, but various characteristics of the larvae, nesting biology and adults also do not fit the usual anthophorid patterns. McGinley and I will treat this matter elsewhere.

Cursory examination of the internal anatomy of the female metasoma of these taxa revealed considerable variation, not only in ovarian anatomy, egg size, and egg shape, but also in overall ovarian size, and size and configuration of the Dufour's gland, all features that should encourage more thorough study of the internal anatomy of a greater number of taxa of bees.

As an offshot of this investigation, the morphology of the oocytes (Fig. 1) of

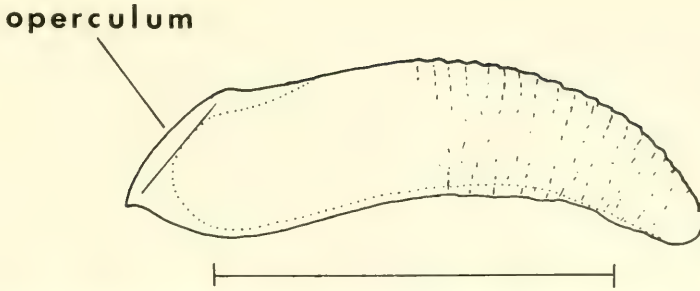


Fig. 1. *Oreopasites vanduzeei*, oocyte, side view with anterior end at left. Scale = 0.5 mm.

the cleptoparasitic *Oreopasites vanduzeei* was of special interest. *Oreopasites*, among other members of the tribe Ammobatini, folds the egg back on itself during oviposition into the cell wall so that the anterior part of the egg comes nearly into contact with the posterior part. The deposited egg is not unlike a sausage bent into a U, and its oblique anterior end (operculum) is flush with the cell wall. In the present study, I observed that the operculum and anterior part of the oocyte were sclerotic and faintly pigmented, whereas the posterior end was transversely corrugated, especially above, and more membranous. Oocytes were only slightly curved and not U-shaped. All oocytes were clearly oriented with their anterior ends pointed anteriorly in the females; and their posterior ends, arranged to descend first through the common oviducts. The corrugations in the chorion of the posterior end of the oocyte probably provide the necessary flexibility for egg bending at oviposition.

Material studied: *Ptiloglossa arizonensis* Timberlake, Portal, Cochise Co., Arizona, September 3, 1982 (J. G. Rozen). *Megandrena mentzeliae* Zavortink, 13 mi NW of Las Vegas, Clark Co., Nevada, May 17, 1980 (J. G. & B. L. Rozen). *Cephalurgus anomalis* Moure & Oliveira, Cosmopolis, São Paulo, BRAZIL, January 27, 1974 (F. C. Thompson), nest #3. *Meliturgula minima* Friese, 22 km ESE of Seeis, SOUTH WEST AFRICA (NAMIBIA), March 15, 1976 (J. G. & B. L. Rozen), all from nest #2. *Nomadopsis barbata* Timberlake, 3 mi S of Hilmar, Merced Co., California, May 3, 1961 (no collector). *Panurgus intermedius* Rozen, Qued Cherrat, 32 km SW of Rabat, MOROCCO, April 21, 1968 (J. G. Rozen & E. Suissa). *Perdita* new species near *wootoniae* Cockerell, Ft. Robinson, Dawes Co., Nebraska, August 11, 1972 (J. G. Rozen & R. J. McGinley), from same nest. *P. portalis* Timberlake, 1 mi N Rodeo, Hidalgo Co., New Mexico, August 30, 1970 (J. G. Rozen). *Meganomia gigas* Michener, 52 km SW Omaruru, SOUTH WEST AFRICA (NAMIBIA), March 27, 1976 (B. L. Rozen). *Macropis nuda* (Provancher), Huyck Preserve, Rensselaerville, Albany Co., New York, July 16, 1978 (J. G. Rozen & N. Jacobson), on flowers of *Apocynum*. *Fidelia villosa* Brauns, 30 km SE Keetmanshoop, SOUTH WEST AFRICA (NAMIBIA), October 23, 1968 (J. G. Rozen). *Kelita chilensis* (Friese), Peñuelas, Valparaiso Prov., CHILE, October 28, 1969 (J. G. Rozen). *Oreopasites vanduzeei* Cockerell, 3 mi S of Hilmar, Merced Co., California, May 3, 1969 (no collector), associated with *Nomadopsis barbata*. *Exomaloposis solidaginis* Cockerell, 20 mi S Animas, Hidalgo Co., New Mexico, September 13, 1977 (J. G. & B. L. Rozen). *Pararhophites orobinus* (Mo-

rawitz), Killi Sarda, 12 km S Quetta, Baluchistan, PAKISTAN, May 14, 1984 (J. G. Rozen, S. Lodhi, R. J. McGinley, I. Stupakoff).

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ETHOLOGY OF *ASILUS GILVIPES* (HINE) (DIPTERA: ASILIDAE)
ASSOCIATED WITH SMALL MAMMAL BURROWS IN
SOUTHEASTERN WYOMING¹

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Abstract. — Ethological studies reported in the literature on *Asilus gilvipes* (Hine) are fragmentary. This study gives a more complete picture of its behavior and ecology. *Asilus gilvipes* feeds, mates, and oviposits in or near the entrance to mammal burrows. The predominant prey are calliphorid flies. Males mate up to six times and females up to eight times, but the same partners were not seen to mate together more than once. Oviposition was observed, with the egg or eggs being dropped into a burrow tunnel. Larvae presumably develop in the burrows since newly emerged adults were retrieved from burrows. No burrow exposure preference to any of the eight compass orientations was noted for *A. gilvipes*. Coexistence with another burrow-inhabiting robber fly *A. formosus* is reported.

In his recent treatise on the Asilini of western United States, Martin (1975) was unable to place *Asilus gilvipes* Hine and *A. formosus* Hine in either new or existing genera. In this paper, they are retained in *Asilus* even though Martin believed that the genus does not occur in the New World. Both species are inhabitants of small mammal burrows on open rangeland (James, 1941), but behavioral and ecological information concerning the two species is fragmentary, with most observations on *A. gilvipes* (Bullington and Lavigne, 1980; Lavigne, 1968; Rogers and Lavigne, 1972). In this study we provide more complete information on *gilvipes* species and limited observations on *A. formosus*.

METHODS AND STUDY AREA

Asilus gilvipes was studied 7.5 km west of the University of Wyoming campus, Laramie, in an abandoned alfalfa field close to State Highway 230 (elev. 1849 m). The study area was 9463 m² in size and contained a large number of Richardson ground squirrel (*Spermophilus elegans* Richardson) and badger (*Taxidea taxus* Waterhouse) burrows. The dominant plant species in the study area were: alfalfa, white top (*Cardaria draba* (L.) Desu.), and bull thistle (*Cirsium vulgare* (Savi) Tenore).

Asilus gilvipes was studied in this habitat between 25 June and 3 August during

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the summers of 1980 and 1981. Studies were conducted from 0700 and 1800 hours daily during both summers, with specific burrow associational data and fly behavioral patterns recorded at hourly intervals. Asilids were marked individually with Testors® enamel on the prothorax for identification purposes so that each individual could be followed or subsequently located. By recapturing marked individuals, we were able to determine adult longevity, length of burrow occupancy, and whether individuals ordinarily mated more than once.

Prey records were obtained by capturing a feeding asilid in an insect net and removing the prey after the asilid dropped it. The asilid was then measured, and its sex and identification number were recorded before released. The prey was subsequently measured and identified in the laboratory.

In early June of 1981, before *gilvipes* emerged, 100 Richardson ground squirrel and 71 badger burrows were sampled for mean burrow entrance diameters and exposure of entrance slopes at eight compass orientations. These burrows were marked individually with a 5 inch nail, with identification numbers placed on the nail head. Subsequent asilid behavioral data taken from sampled burrows facilitated burrow size preference analysis.

Because the use of the burrows by the asilid may be an adaptation to a harsh environment, we were interested in determining what temperature differential existed between the soil surface and the burrow interiors. Soil temperatures were taken with a Soil Test Inc. metal thermometer (6-201), at 3 cm depth at the soil surface and at 3 cm depth in randomly selected burrows. Each day we recorded hourly the temperature of different burrows.

RESULTS AND DISCUSSION

Seasonal distribution and abundance.—A total of 742 *gilvipes* were marked and released during the 1981 season. Of these, 451 (61%) were recaptured or observed on one or more days within the study area. Marked flies showed a strong affinity for the study area throughout the season. Sampling outside the immediate study area revealed the presence of only two marked specimens.

Following marking, individuals survived an average of 17 days; the longest lived individual was recaptured after 23 days (Fig. 1). This suggests that adult flies normally survive for approximately three weeks. Similar findings for this species were found by Rogers and Lavigne (1972) in northeastern Colorado.

Asilus gilvipes is a short lived early/midsummer species in southeastern Wyoming (Fig. 2). In 1981 the first adults appeared on 25 June (4 ♀, 1 ♂ Emergence continued over a short span of time with the population peaking on 10 July (25 ♀, 33 ♂). The population remained at high density through mid-July and then decreased; a secondary peak in abundance was noted on 25 July (20 ♀, 16 ♂), followed by a steady decline with no individuals recovered after 2 August. Censuses conducted the previous year provided similar results for population abundance and time of last adult sighting.

Recaptures of *gilvipes* were most numerous around mid-July when individuals were most abundant. Daily sampling showed that as the population rose and fell, sexual density followed the population curve; the ratio of one sex to the other remained the same (49:51%, $N = 742$) throughout the season ($\chi^2 = 3.1$ N.S.). For *Edioctria tibialis* Banks, however, Scarbrough (1981) found that males were more abundant than females during the early half of the season, whereas the reverse was true in the latter half.

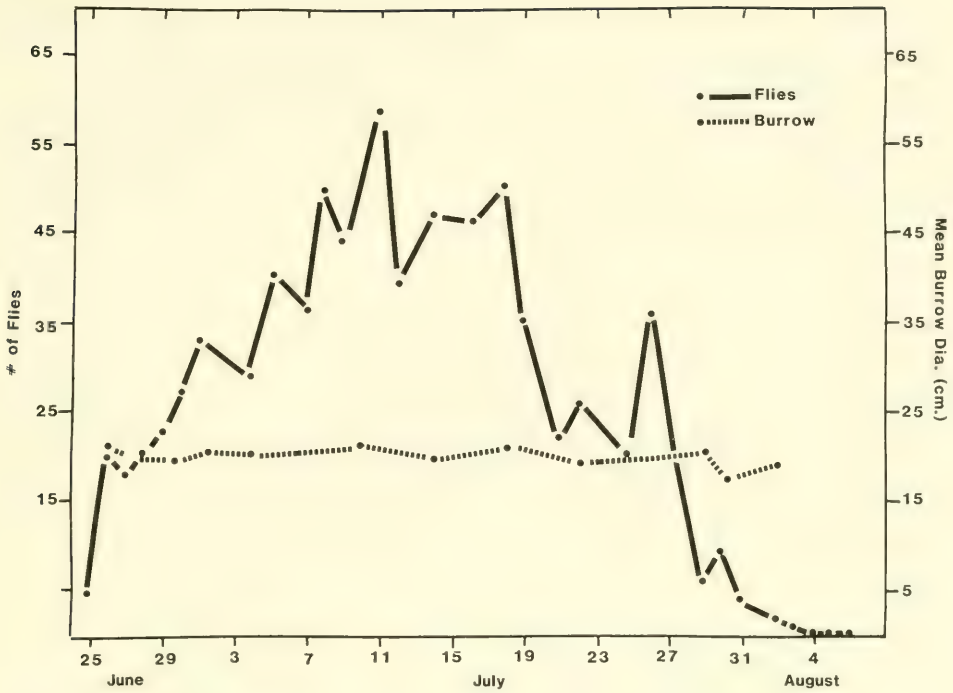


Fig. 1. Relative abundance of *Asilus gilvipes* and mean burrow diameter.

Diurnal behavior.—On most days, *gilvipes* was found resting either within burrows or on the outer rim. Individuals would remain associated with a specific burrow for varying numbers of days. The longest association was 3 days.

Predation was the most common activity observed during most daylight hours with the exception of 1300–1400 h when mating behavior was dominant (Fig. 3). Predation took place within the confines of the burrow when burrow temperatures ranged from 16.5–27.0°C. The peaks of predatory activity occurred at 1100–1200 h and again at 1400 to 1500 h MDT. These peaks, which correspond to soil surface temperatures of 21–33° and 23–36°C, may be associated with increased density of potential prey within the burrows. We postulated that these insects were escaping from high outside temperatures by entering the burrows (Lavigne, 1968). The majority of prey were taken while they were in flight within the burrow, but insects were also captured as they entered and left the burrow.

Grasshopper nymphs were also taken as prey. Apparently these wingless insects were captured while resting on the burrow walls. To test this assumption, a tabanid fly, *Tabanus* sp., was captured and one of its wings removed. The tabanid was then placed on the inside rim of a *gilvipes*-occupied burrow. Twenty-two minutes later a specimen of *gilvipes* was found feeding on the tabanid.

Following is a description of a typical predatory act recorded on 12 July 1980.

3:22 pm A *gilvipes* female observed in a badger burrow with a western exposure (entrance diameter of approx. 15 cm); hovers within burrow and captures a flying calliphorid; flies to northern rim. The prey is impaled on the hypopharynx and held by the midlegs.

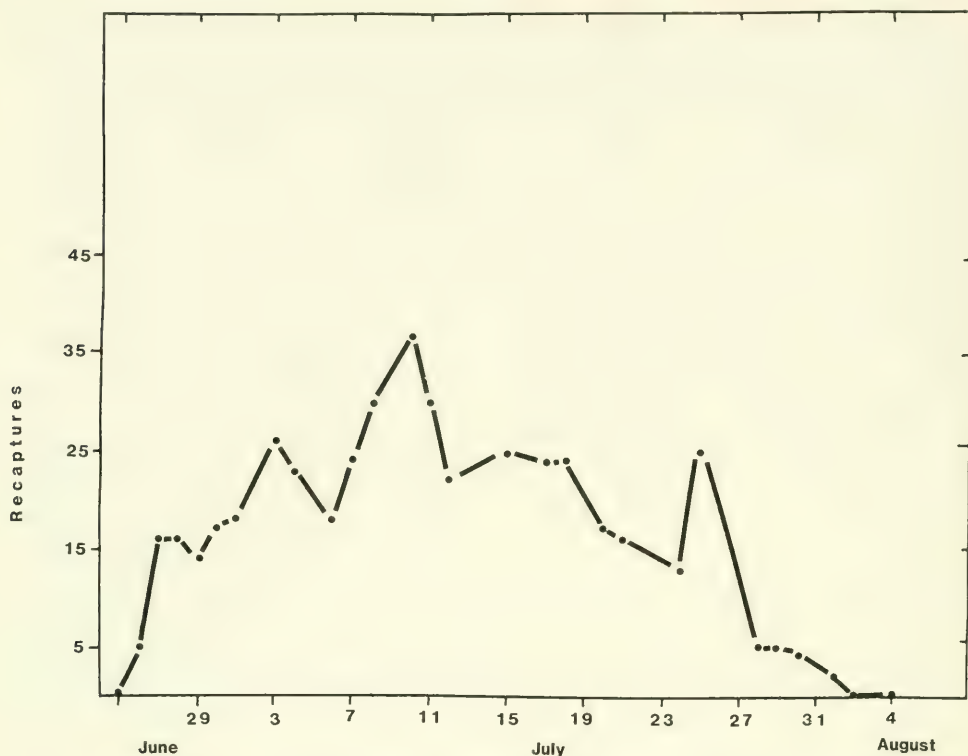


Fig. 2. Numbers of *A. gilvipes* recaptured one or more day(s) following mark and release.

- 3:22:30 Hovers; moves hypopharynx to dorsum of prey's thorax and returns to burrow wall.
- 3:27 Hovers; places hypopharynx in the ventral portion of calliphorid's abdomen, returns to burrow wall.
- 3:31 Hovers; places hypopharynx in the pleural section of the thorax; returns to burrow wall surface.
- 3:46:30 Hovers; shifts hypopharynx to venter of abdomen; returns to burrow wall; ballooning of prey evident.
- 3:57 Hovers; moves hypopharynx to venter of thorax; returns to burrow wall.
- 4:09:15 Hovers; shifts hypopharynx to dorsal tip of abdomen.
- 4:19 Prey falls off hypopharynx; no tarsal assistance.

Complete feedings from capture to release were observed for 15 prey. The mean feeding time was 43 minutes, ranging from 5–72 minutes in duration. The majority of prey taken were Diptera (Tables 1–2); these were primarily *Phormia regina* Meigen. Diptera were 33% of the prey of *Asilus mesae* (Tucker) (Rogers and Lavigne, 1972). Dennis and Lavigne (1975) found that Diptera made up 18.6% of the prey of *A. mesae*.

Because there was an apparent specificity for one group of flies, the authors proposed the following hypothesis. Calliphorids deposit eggs on dead carcasses

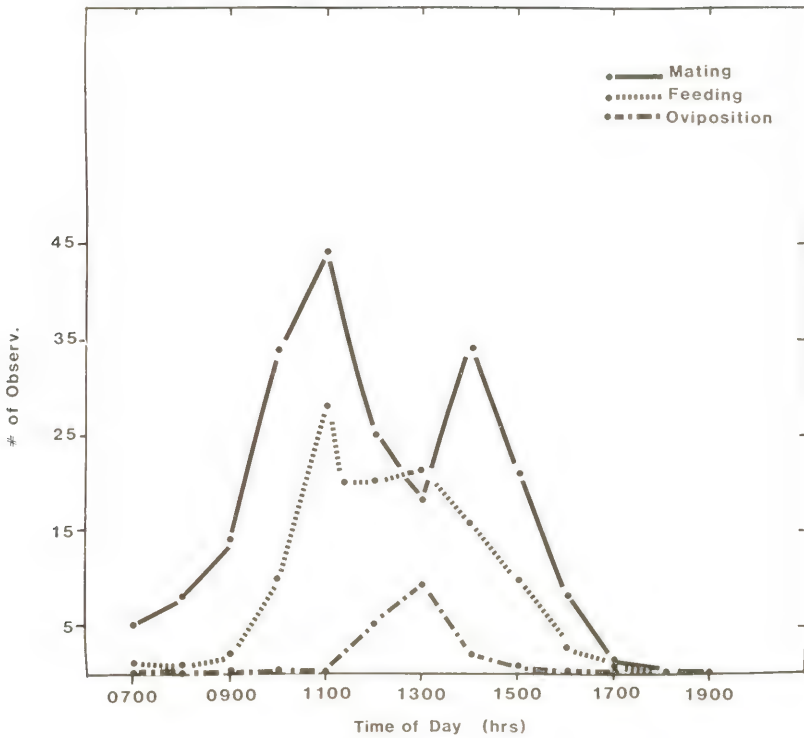


Fig. 3. Diurnal rhythm of mating, feeding, and ovipositional activity of *Asilus gilvipes* (mating N = 111, feeding N = 212, oviposition N = 171).

and other decaying organic materials, such as feces (Hall, 1948). Badgers and ground squirrels are known to defecate in and near their burrows (F. Lindzey, Utah State University, pers. comm.; Sargent and Warner, 1972; Messick and Hornocker, 1981). It follows that calliphorids have a high selection value because they are attracted to dung and/or to odors emanating from it, thus increasing the density of flies in the burrow microhabitat.

As a preliminary test we attempted to associate mammal burrow occupancy with burrow visitation by calliphorids. To detect burrow occupation by mammals, an experiment was conducted in which grass stalks were placed upright about 6 cm deep in burrow tunnels occupied by *A. gilvipes* during that day. This method has been used by some badger ethologists to check for burrow occupancy (Lindzey, 1978). The following morning the grass stalks were checked to see if they had remained upright. A total of 25 badger burrows were “grass stalked” on 8 July 1981. The following morning, 9 July, stalks in 18 burrows were knocked down. This preliminary test indicated that the burrows were occupied, but did not definitely identify the species of mammal inhabiting them, since ground squirrels have been known to inhabit badger burrows (H. Harlow, Univ. of Wyoming, pers. comm.). On 10 July two artificial burrows were dug measuring 8–10 cm in depth with burrow diameters of 11 cm and 13 cm, respectively. Fresh dung pellets were collected from ground squirrel-occupied burrows and placed in one of the burrows. Dung from ground squirrels was utilized because of its abundance, freshness and

Table 1. Number and percent composition of prey by insect order taken by *Asilus gilvipes*.

Order	Male		Female		Total	
	Number	Percent	Number	Percent	Number	Percent
Coleoptera	5	6.0	6	5.0	11	5.4
Diptera	72	86.7	106	88.3	178	87.7
Hymenoptera	5	6.0	2	0.6	7	3.4
Orthoptera	1	1.4	6	5.0	7	3.4
Total	83	99.7	120	99.9	203	99.9

availability (badger dung is placed in special pockets in the burrow itself by the badger (Messick and Hornocker, 1981) whereas ground squirrel dung is available at the burrow entrance). Calliphorids on the rim and within each burrow, one containing feces and the other not, were counted hourly throughout the day. On the following day, fresh dung was placed in the burrow lacking it and the previous day's dung was removed from the burrow which had contained it. Calliphorid and muscoid flies were observed only in the artificial burrow containing the dung. This simple experiment, although not replicated, suggests that the high number of calliphorid flies in the diet of this species of asilid is due to the propensity of these flies to congregate in the vicinity of dung, a behavior to which the asilids appear to have adapted successfully.

The mean predator to prey size ratio for this species is 2.03:1 (Table 3), based on length. Females, though not significantly larger than males took similar sized prey which resulted in a significantly greater prey ratio for them. While *Efferia frewingi* females have been shown to be more discriminate than males in prey choice based on models presented to both sexes (Dennis et al., 1975), the data in Table 4 suggest that this is not the case for *A. gilvipes*. Females in fact appear to be less discriminatory, especially for the larger size class. However, the 15.1+ mm size class are two reports of cannibalism by females on males.

Reports of cannibalism are not unusual among the Asilidae (Lavigne and Dennis, 1975; Rogers and Lavigne, 1972; Lavigne and Holland, 1969) but its cause is obscure. Fox (1975), in discussing cannibalism in general, states that it is not an "aberrant behavior" limited to stressed populations, but a normal response to many environmental factors. Intense crowding is one factor suggested by Fox but such was not the case in this study. The availability of potential prey may be the

Table 2. Number and percentage of Diptera prey taken by *Asilus gilvipes*.

Family	Male		Female		Total	
	Number	Percent	Number	Percent	Number	Percent
Anthomyiidae	2	1.1	1	0.5	3	1.6
Asilidae	2	1.1	3	1.6	5	2.8
Calliphoridae	61	34.3	90	50.5	151	84.8
Muscidae	—	0.0	5	2.8	5	2.8
Therevidae	1	0.5	1	0.5	2	1.1
Sarcophagidae	2	1.1	3	1.6	5	2.8
Undet. Diptera	4	2.2	3	1.6	7	3.9

Table 3. Relation between length of *Asilus gilvipes* and that of its prey.

Sex	Predator Length (mm) ¹			Prey Length (mm)			No. of Prey Measured	Mean Ratio of Predator to Prey
	Min.	Max.	Mean	Min.	Max.	Mean		
Male	14.0	21.0	17.00	3.50	13.50	8.54	61	1.99 ^b
Female	17.0	23.0	18.20 ^a	3.00	17.20	8.65	96	2.10 ^c
Total	14.0	23.0	17.60	3.0	17.20	8.60	157	2.03

¹ 45 measured of each sex.
^a Not significant difference; $P = .05$ df 44.
^b Significant difference; $P \leq .05$ utilizing t -test approx. variance formula for a ratio.
^c Significant difference; $P \leq .05$ utilizing t -test approx. variance formula for a ratio.

more valid reason. *Asilus gilvipes* females were observed to feed on the males when population density was low (24 July). Many of the burrows at this time were poorly maintained, indicating less burrowing rodent activity in the area. This could have resulted in fewer visits by coprophagous flies. Additionally, calliphorid prey records were fewer late in the asilid season.

Mating behavior.—Mating behavior of *A. gilvipes*, tail to tail in this species, has been described in detail previously by Bullington and Lavigne (1980). Twelve complete matings of *A. gilvipes* were observed during the present study. They ranged from 18 to 42 min. in duration with the mean being 26.5 min.

Multiple mating as observed by Bullington and Lavigne (1980) appears to be a common behavioral attribute of this species. Sixty marked males were observed to mate from 1 to 6 times, a mean of 1.33 mating/male. Additionally, 53 marked mated females were recorded mating 1 to 8 times for a mean of 1.47 matings/female, but no instances are recorded of the same male and female remating.

Oviposition behavior.—Following 48 observed matings, females oviposited immediately in only 20 instances. Those that did may have mated previously.

While resting on the rim of the burrow, the female drops eggs either singly or in small packets of three into the burrow tunnel. The time spent ovipositing by females ranged from 2–12 min. (mean 3.5 min.). The eggs presumably hatch within the burrow and the larvae feed within the burrow until pupation. Two newly emerged *A. gilvipes* adults were seen to emerge from badger burrows (4 July, 8 July 1981); pupal cases were recovered from the burrow.

Burrow preference.—Since *Asilus gilvipes* is intimately associated with mammal burrows, it was of interest to determine if the flies exhibited preference for certain types of burrows. Marked individuals were associated for varying time periods with 133 burrows. Of these, 15 asilids were found in ground squirrel burrows and 116 in badger burrows. The average diameter of the entrance of ground squirrel

Table 4. Size class percentage of prey of *Asilus gilvipes* by sex.

Sex	Prey Size				Total Prey
	3.1–7.0 (mm)	7.1–11.0 (mm)	11.1–15.0 (mm)	15.1+ mm	
Male	17.0%	79.0%	3.0	0.0%	61
Female	21.0%	74.0%	3.0	2.0%	96
Avg. total %	19.0%	76.5%	3.0%	1.0%	157

Table 5. Chi-square 8×2 contingency table test results comparing expected frequencies with observed frequencies for burrow occupation of *Asilus gilvipes* at eight compass orientations.

	N	NW	NE	S	SW	SE	E	W
Observ. bur.	42.00	16.00	18.00	27.00	19.00	12.00	48.00	53.00
Expected bur.	49.58	14.16	15.45	28.97	14.81	12.23	44.42	55.37
Ob. <i>A. gilvipes</i>	35.00	6.00	6.00	18.00	4.00	7.00	21.00	33.00
Ex. <i>A. gilvipes</i>	27.42	7.84	8.55	16.03	8.19	6.77	24.58	30.63

$$\chi^2 = 9.9113, df = 7, P = .05.$$

burrows was 12.80 cm and that of badger burrows was 20.54 cm, for an overall average of 18.69 cm. No correlation was found between the expansion of the size of the population and the choice of burrow (Fig. 1). We assume this to mean that there were always more burrows available than flies present, so no inter- or intraspecific competition for burrows occurred.

Additionally we were interested in knowing whether there was any correlation between compass direction of the burrow entrance and the choice of burrow made by *A. gilvipes*. In Table 5, an 8 by 2 contingency table of burrow occupancy by *A. gilvipes* at eight compass orientations shows that no preference for any burrow exposure existed ($P > 0.05$). Lavigne (1968) and Rogers and Lavigne (1972) stated that asilids use burrows to escape the heat. We find that burrows are used in times of high winds and storms as shelters, as well as during periods of high air temperatures.

Species coexistence.—Only one other species of robber fly, *A. formosus* Hine, utilized burrows on the same study site. This species was previously described as a burrow resident by Rogers and Lavigne (1972) in northeastern Colorado. They speculated that coexistence of the two species of asilids might occur under the right circumstances. While the two species occupy the same burrows in the same habitat, they differ in their seasonal occurrence. *Asilus gilvipes* is present from 25 June to 3 August, whereas *A. formosus* is present from 12 July to late August. They also differ in size, with *A. gilvipes* at 17.60 mm in length, being significantly larger than *A. formosus* (14.50 mm) ($P < 0.05$ *t*-test). This size difference allows the two species to share the available prey, with *A. gilvipes* taking the larger prey items. There also exists a significant difference in the mean diameter of the burrow opening chosen by each species: those of *A. gilvipes* measure 18.69 cm, whereas *A. formosus* inhabits burrows measuring 10.32 cm in diameter. Consequently, it appears that these two species can be present in the same habitat because they differ in seasonal occurrence, size, and burrow preference. Similar coexistence strategies with respect to robber flies have been noted by other authors (Dennis and Lavigne, 1975; Lavigne and Holland, 1969; Rogers and Lavigne, 1972; Scarbrough, 1981).

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**CORRECT NAMES FOR SPECIES OF *TACHYSPHEX* OBSERVED
BY EVANS (1970) AT JACKSON HOLE, WYOMING, WITH NEW
INFORMATION ON *T. ALPESTRIS* AND *T. SEMIRUFUS*
(HYMENOPTERA: SPHECIDAE)**

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Abstract.—The correct names are given for the five species of *Tachysphex* observed by Evans (1970) at Jackson Hole, Wyoming. Additional nesting information for *T. alpestris* and initial observations on *T. semirufus*, both based upon Evans' field notes, are detailed.

In 1970 Evans presented information on the nesting behaviors of five species of *Tachysphex* from Jackson Hole, Wyoming. The names provided for two of the species, *T. aethiops* (Cresson) and *T. tarsatus* (Say), are correct but the names of the three other species are incorrect. The purpose of the present paper is to correct the species names, utilizing W. J. Pulawski's determinations, and to report new information on one of the species, *T. alpestris* Rohwer, and on a previously unreported species, *T. semirufus* (Cresson), using H. E. Evans' field notes. This information is thus made available for inclusion in Pulawski's forthcoming revision of the North and Central American species of *Tachysphex*.

T. pauxillus Fox is the correct name for *T. nigrior* Fox (Pulawski, in Krombein, 1979). The behavior of this species (Evans, 1970) is very similar to that of *T. tarsatus* (see Williams, 1914). In fact Evans referred to this species in his Biological note no. 2129 as behaving "exactly like *tarsatus*, but . . . all black," because it captured a relatively large acridid, carried it on the ground into an open entrance, and stored only one prey in a single-celled nest.

Two of the other species observed by Evans (1970), *T. sp. near linsleyi* Bohart and *T. terminatus* (Smith), are actually *T. clarconis* Viereck and *T. alpestris*, respectively. Both species are members of the distinctive *terminatus* species group (Krombein, 1979), and, based upon Evans' ethological descriptions, both resemble *T. terminatus* in their nesting behaviors. Recently, Elliott and Kurczewski (1985) confirmed Evans' observations on *T. clarconis*. Both authors noted provisioning flights by the wasps, temporary closure of the nest entrance, and storage of several acridid nymphs per cell. In addition, Evans (1970) reported a two-celled nest for this species and Elliott and Kurczewski (1985) described leveling of the tumulus.

Evans (1970) noted *T. alpestris* (as *T. terminatus*) preying on small acridid nymphs, storing several per cell, making a temporary closure of the entrance, and

constructing a three-celled nest. Elliott and Kurczewski (1985) substantiated the use of nymphal Acrididae as prey of *T. alpestris*, and Evans' field notes [nos. 2016 (not 2013, as reported), 2033] provide additional behavioral information on this species. Prey transport was by flying and the three-celled nest contained three (no egg), two (egg), and 13 (egg) prey per cell, respectively. The burrow lengths were 5 cm for a single-celled nest and 8–10 cm for the three-celled nest.

The junior author (Biol. note no. 1989) also observed a female of *T. semirufus* (det. W. J. Pulawski) at Jackson Hole, Wyoming, but this observation was not reported in Evans (1970). The wasp proceeded forward on the ground, holding her prey with the mandibles by the bases of its antennae. She apparently did not use any of the legs to grasp the prey's body. Instead, she used her wings to assist in transport but did not attempt to fly. The wasp carried the prey about 5 m in a rather straight line directly into an open burrow. Two minutes later, she appeared headfirst in the entrance and began raking sand backward into the burrow. She came out 1–2 cm, backed into the tunnel, and packed in the sand, using directed blows from the end of the abdomen. In seven minutes the female had completed the closure by filling the burrow with the sand from the tumulus, but she left the entrance depressed slightly below the sand surface.

The burrow (ca. 3 cm long) entered obliquely the sandy soil mixed with stones, curved sharply, and ended in a cell about 1 cm deep. The single prey, a nymphal mormon cricket, *Anabrus simplex* Haldeman (Tettigoniidae) (det. A. B. Gurney) was placed in the cell in a head inward position. The wasp's egg was placed on the venter of the prey's thorax, possibly between the first two pairs of legs.

W. J. Pulawski (pers. comm.) has seen a specimen of *T. semirufus* pinned with a nymphal *Capnobates* sp., probably *occidentalis* (Thomas) (Tettigoniidae). These are the only prey records known for this species of *Tachysphex* and they indicate a specificity for long-horned grasshoppers.

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**STETHOCONUS JAPONICUS (HETEROPTERA: MIRIDAE): A
PREDATOR OF STEPHANITIS LACE BUGS NEWLY DISCOVERED
IN THE UNITED STATES, PROMISING IN THE BIOCONTROL OF
AZALEA LACE BUG (HETEROPTERA: TINGIDAE)**

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Abstract. — The first Western Hemisphere record of the predatory Japanese plant bug *Stethoconus japonicus* Schumacher is reported based on specimens collected in four localities in Maryland. Established populations of this potentially useful, adventive, obligate predator of *Stephanitis* lace bugs were discovered preying on the azalea lace bug, *Stephanitis pyrioides* (Scott), also native to Japan. Predatory habits of species in the genus are reviewed, the adult is redescribed and illustrated, and information to help separate *japonicus* from other Nearctic Miridae is provided. The genus *Stethoconus*, previously placed in the tribe Clivinemini of the subfamily Deraeocorinae, is transferred to Hyaliodini also in the Deraeocorinae.

During 1985 while studying the field biology of the azalea lace bug, *Stephanitis pyrioides* (Scott), one of us (KMG) discovered a population of an unrecognized plant bug on an isolated, U.S. grown, potted azalea in Beltsville, Maryland. Initial observations indicated that adults and nymphs were preying on the lace bugs. Eventual study of these specimens revealed that the mirid was *Stethoconus japonicus* Schumacher, known only from Japan.

Herein, we review the literature discussing the predatory habits of species in *Stethoconus* Flor, give the first distribution and host records of *S. japonicus* in North America, redescribe and illustrate the adult, and provide information to help separate this species from all other Nearctic Miridae, including a clarification of the tribal and subfamily placement and its transfer to the tribe Hyaliodini in the subfamily Deraeocorinae.

This report was prepared to alert others studying azalea lace bug of the occurrence of this potentially important predator in the United States.

PREDATORY HABITS IN THE GENUS *STETHOCONUS*

The mirid genus *Stethoconus* contains eight Old World species, of which only two African species are not yet proven exclusive predators of lace bugs or Tingidae (Carayon, 1960). The species now included in *Stethoconus* are: *bimaculatus* (Schouteden), 1946, known from Africa ["Burunga, Luenga, and Mikenno volcano"]; *cyrtopeltis* (Flor), 1860, from northern Europe; *distanti* (Schouteden),

1946, from Africa ["Abimva"]; *frappai* Carayon, 1960, from Madagascar; *japonicus* Schumacher, 1917, from Japan; *praefectus* (Distant), 1909, from India and Sri Lanka; *pyri* (Mella), 1869, from southern Europe and western Transcaucasia; *scutellaris* (Schouteden), 1946, from Africa ["Rutshura"].

Stethoconus pyri (Mella) [most frequently cited as *Stethoconus cyrtopeltis* (Kerzhner, 1970)], one of the better known species, is closely associated with the pear lace bug, *Stephanitis pyri* (Fabricius), found on various fruits, including apple, apricot, peaches, and pears, and other trees such as hawthorn, linden, and mountain ash (Carayon, 1960). Wagner (1970) illustrated the adult dorsal habitus, head, and claws [as *cyrtopeltis*]. Rey (1881) remarked that the predatory nymphs of *Stethoconus pyri* [as *Stethoconus mamillosus* Flor, 1861] closely resembled the appearance, coloration, and movements of *Stephanitis pyri* nymphs to the extent that he declared them "mimics." Gautier (1927) observed that *Stethoconus pyri* [as *cyrtopeltis*] uses its front legs to hold *Stephanitis pyri* and does not abandon its prey until it is completely empty of fluids. He reported also that a single nymph of this mirid could destroy more than 20 lace bugs in a single day. In the USSR, Puchkov and Puchkova (1957) also observed that individuals of *Stethoconus pyri* [as *cyrtopeltis*] use their anterior legs to hold prey against the leaf surface of linden, randomly probe with their rostrum, and feed until the lace bug is drained. They reported that a 3rd instar nymph could destroy 5–10 or more 1st and 2nd instar *pyri* nymphs in 24 hours. Golfari (1937) considered *Stethoconus pyri* [as *cyrtopeltis*] the most important predator attacking *Stephanitis pyri* in central Italy, followed by anthocorids, nabids, and a mymarid egg parasite.

In northern Europe where *Stephanitis pyri* is absent, Schumacher (1917) suggested that *Stephanitis oberti* Kolenati served as the host of *Stethoconus cyrtopeltis*. This information is probably the only correct prey association for *cyrtopeltis*. Kerzhner (1970) illustrated male parameres and provided a key to separate *Stethoconus cyrtopeltis* from *Stethoconus pyri*.

Stethoconus praefectus (Distant) is a major predator of a coconut palm lace bug, *Stephanitis typicus* Distant, in India. Mathen et al. (1967) first noted for *praefectus* [as *Apollodotus praefectus*] "that the swift-moving, milk-white predatory nymphs were available in large numbers . . ." on coconut seedlings and, in the laboratory, they fed on all stages of the coconut lace bug, *Stephanitis typicus*, at the rate of one to seventeen nymphs per predator nymph per day. Mathen and Kurian (1972) studied the life history in more detail and described and illustrated the life stages. In that study, 54 to 74 lace bugs were consumed during nymphal development, and adults consumed an average of slightly more than 5 lace bugs per day, a significant number considering that this bug breeds throughout the year and females potentially produce more than 50 eggs during their life cycle.

Cheng (1967), in studying the ecology of *Stephanitis typicus* on banana in Taiwan, reported that a *Stethoconus* sp. [possibly *praefectus*] could be found throughout the year, except December and January, and that females of this predatory species deposited an average of 34 eggs in 8–10 days. He further noted that a single specimen of this species destroyed about 356 tingids during its life.

Less is known about the African species of *Stethoconus* but at least two are known to feed on tingids. *Stethoconus scutellaris* (Schouteden) from the Zaire (previously Belgian Congo) is said to be an important predator of coffee tingids in the genus *Habrochila* (Carayon, 1960). More recently, Carayon (1960) described

the new species *Stethoconus frappai* from Madagascar, which was found preying on a coffee tingid, *Dulinius unicolor* (Signoret). Decazy (1975), in studying the control of *D. unicolor*, noted that *frappai* afforded some degree of control when lace bug populations were high and recommended special timing of insecticide applications to avoid affecting predator levels.

Stethoconus japonicus Schumacher

No detailed life history data are available for *japonicus*. Nawa (1910) reported that its habits [as *Capsus* sp.] in Japan were similar to those of *cyrtopeltis* and *praefectus* and provided illustrations of the adult (including the antenna, rostrum, legs, wings, and genital capsule) and a figure of a nymph feeding on *Stephanitis ambigua* Horvath [as *Stephanitis pyrioides* (Scott); clarified by Schumacher, 1917]. Esaki (1932) illustrated the adult and noted that this beneficial species also preys on *Stephanitis nashi* Esaki and Takeya. Kerzhner (1970) illustrated the male parameres.

Our observations in Maryland indicate that *japonicus* is a voracious predator of azalea lace bug and, although both species are native to Japan, this report may be their first predator-prey association (Oliver et al., 1985). The literature leaves little doubt that all members of the genus *Stethoconus* are specialized predators of Tingidae; all but the African species appear to prefer lace bugs of the genus *Stephanitis*. Reports of prey consumption for *pyri* and *praefectus* indicate that members of the genus are potentially important biological control agents that could be used in integrated pest management programs. Because *japonicus* is said to have habits similar to those of better known *Stethoconus* species, the presence of large, established populations of this species in the United States could have a significant impact on azalea lace bug control programs. Researchers working with ornamental azaleas should be alert to the presence of this adventive, beneficial species in the United States.

Description of adult (Figs. 1-6).—*Male*: Length 3.58–3.76 mm, width across widest point on hemelytra 1.76–1.84 mm; general coloration yellowish brown with extensive fuscous markings; clothed with rather long, semierect, yellowish pubescence. *Head* (Figs. 1, 2): Length 0.26–0.30 mm, width 0.78–0.80 mm, vertex 0.28–0.30 mm; much wider than long, basal margin distinctly carinate, eyes prominent, not touching anterior margin of pronotum; shiny yellow to yellowish orange, vertex sometimes with an inverted, dark-brown, V-shaped mark extending to bases of antennae, tylus narrowly bordered by dark brown. *Rostrum*: Length 0.96–1.02 mm, extending to middle of prosternum between pro- and mesocoxae; yellowish brown with apex of segment IV fuscous. *Antenna*: Pale yellowish brown, segment I sometimes more yellow to yellowish orange, apical ½ of segment II fuscous; segment I, length 0.30–0.32 mm; II, 1.28–1.34 mm; III, 0.36–0.40 mm; IV, 0.32–0.34 mm. *Pronotum* (Figs. 1-2): Length 0.96–1.00 mm; basal width 1.52–1.56 mm; trapeziform, distinctly convex, evenly and deeply punctate except for shiny depressed calli, area between calli with a somewhat V-shaped carina; areas between punctures on disc appearing calloused, callouses coalescing in some areas to form small bumps or blunt tubercles, collar wide, punctate, about 0.16–0.18 mm long at meson; lateral margins rounded, straight in dorsal aspect, with a distinct, narrow carina on propleura; posterior margin straight through middle with lateral ⅓ angled anteriorly; overall coloration yellowish brown, mesal carina

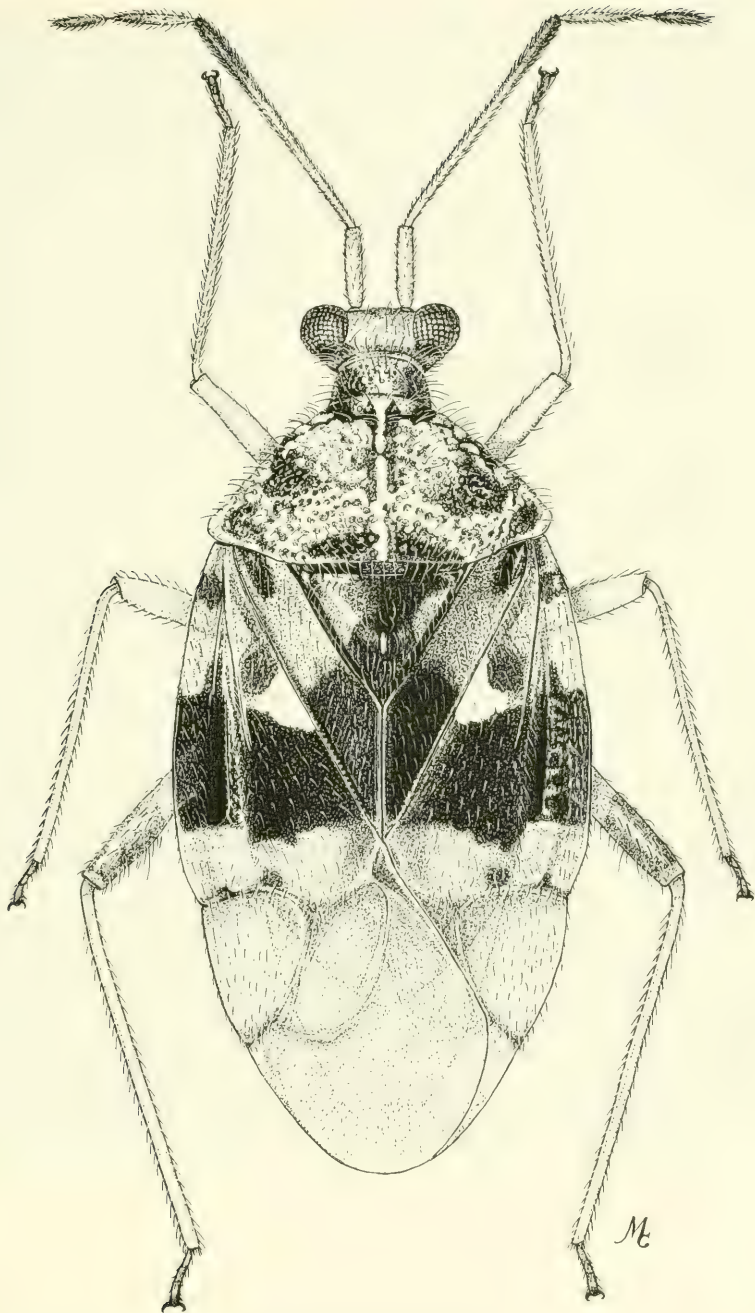
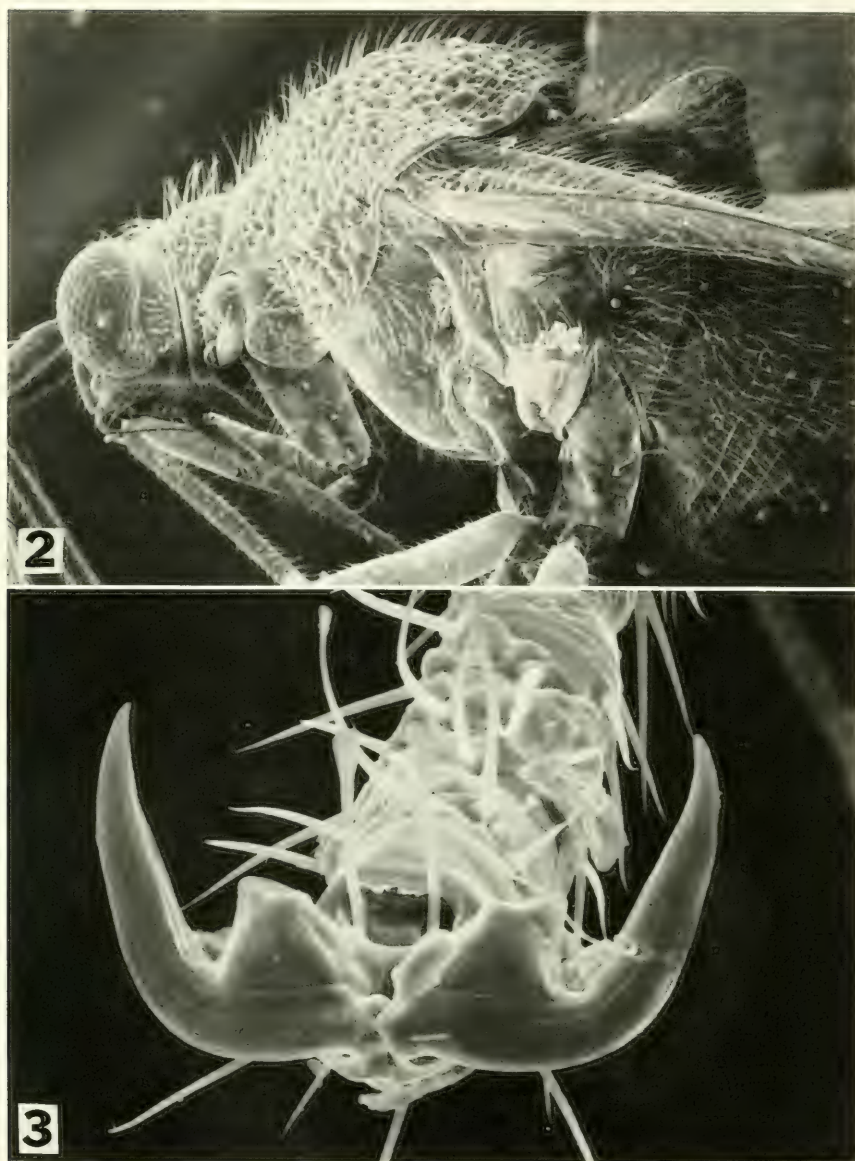


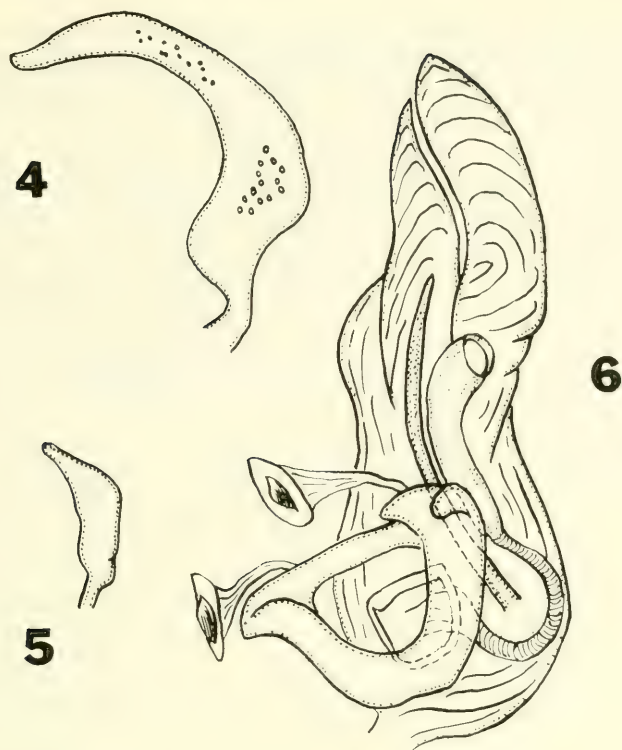
Fig. 1. Adult female habitus of *Stethoconus japonicus*.

and calloused areas between punctures ivory white, two large spots at base of disc on either side of mesal carina, two spots on middle of disc near lateral margins, and area bordering calli dark brown. *Scutellum* (Fig. 2): Shiny fuscous, each side of base with a large yellowish spot; swollen, cone-shaped, nearly pyramidal; apex



Figs. 2, 3. Scanning electron micrographs of *Stethoconus japonicus*. 2, Lateral aspect of head and thorax (48.5 $\times$). 3, Deeply cleft claw (867 $\times$).

laterally compressed. *Hemelytra*: Broadly rounded, embolium wide; generally shiny, yellowish brown with a large, wide, dark-brown to fuscous band through middle of embolium, corium, and clavus, a large, irregular, white spot at middle of corium (anterior to fuscous band) adjacent to clavus, also with a dark brown or fuscous spot at base of embolium, clavus, and on anterior side of white spot, cuneus and apical $\frac{1}{4}$ of corium translucent, tinged with pale brown, apex of cuneus sometimes brown. *Ventral surface*: Thorax shiny, fuscous to black, ostiolar evaporative area and a narrow mesopleural sclerite yellowish; abdomen shiny yellow



Figs. 4–6. Male genitalia of *Stethoconus japonicus*. 4, Left paramere. 5, Right paramere. 6, Aedeagus.

to pale yellowish brown, invaded by darker brown along segment margins and ventral area of basal segments. *Legs*: Uniformly pale yellow, metafemur with a wide, fuscous, subapical band and apex yellow to yellowish orange. *Claws*: Deeply cleft (Fig. 3). *Genitalia*: Left paramere (Fig. 4); right paramere (Fig. 5); aedeagus (Fig. 6).

Female: Length 4.08–4.40 mm, width 2.08–2.12 mm. *Head*: Length 0.40–0.42 mm, width 0.76–0.78 mm, vertex 0.30–0.34 mm. *Rostrum*: Length 1.06–1.14 mm. *Antenna*: Segment I, length 0.36–0.38 mm; II, 1.30–1.32 mm; III, 0.40–0.44 mm; IV, 0.28–0.30 mm. *Pronotum*: Length 1.06–1.16 mm, basal width 1.60–1.74 mm.

Very similar to male in coloration and markings, differing in the larger, more robust size and more broadly rounded hemelytra.

Voucher specimens preserved (all specimens in U.S. National Museum of Natural History, Washington, D.C. [USNM]).—Maryland: 4 ♂, 1 ♀ (plus nymphs), Prince Georges Co., USDA Res. Area (BARC-East), 1–2 Aug. 1985, K. M. Gott and J. W. Neal, Jr., taken on Martha Hitchcock azalea, infested with *Stephanitis pyrioides*; 3 ♂, 6 ♀ (plus nymphs), Prince Georges Co., Rt. 1, 2 mi. E of Beltsville, 21 Aug. 1985, T. J. Henry, on ornamental azaleas infested with *S. pyrioides*; 4 ♂, 8 ♀ (plus nymphs), Prince Georges Co., Laurel, Rt. 194, 21 Aug. 1985, T. J. Henry, on ornamental azaleas infested with *S. pyrioides*. Numerous other individuals observed in the field or kept for laboratory study.

Remarks.—The generic identification of our specimens eluded us early in the discovery of *S. japonicus*. The combination of deeply cleft claws (Fig. 3), with only simple hairs between them and without fleshy arolia, the deeply punctate pronotum (Figs. 1–2) with a wide, punctate collar, and the shiny, translucent hemelytra having a wide embolium, placed our genus in the subfamily Deraeocorinae and the tribe Hyaliadini using Carvalho's (1955) key to the world mirid genera or to *Hyaliodes* Reuter using Slater and Baranowski's (1978) key to the North American mirid genera. Only through persistent perusal of the world genera did it become apparent that our specimens belonged to the genus *Stethoconus*, until recently (Kerzhner, 1964, 1970), inexplicably placed in the tribe Dicyphini of the subfamily Phylinae (Carvalho, 1958) or Bryocorinae (Schuh, 1976). Careful study of the claws, pronotum, hemelytra and male genitalia convinced us that *Stethoconus* was misplaced in the Dicyphini and should be transferred to the subfamily Deraeocorinae.

Eventual discovery of Kerzhner's (1964) transfer of *Stethoconus* to the subfamily Deraeocorinae supported our conclusion of improper placement in the Dicyphini. We disagree, however, with Kerzhner's (1964, 1970) placement of the genus in the tribe Clivinimini. Clivinimines are characterized by a trapeziform pronotum, having a narrow, impunctate, ringlike collar, and the calli of *Clivinema* and *Largidea* are represented by two depressed, shiny areas connected by an impressed, shiny line (Knight, 1968). Species of *Stethoconus* have the pronotum narrowed anteriorly into a wide, punctate collar and lack the depressed, shiny areas of the calli.

In addition to the adult characters given above, examination of the nymphs, having a distinct, elongate anal tube characteristic of the tribe Hyaliadini (Akingbohunge, 1974; Wheeler, 1980) and an abdominal scent gland opening similar to that of species in *Hyaliodes* (Akingbohunge et al., 1973), further supports placement in the Hyaliadini. We, therefore, remove *Stethoconus* from Clivinimini and transfer it to the tribe Hyaliadini in the subfamily Deraeocorinae, with the realization that the tribal classification within Deraeocorinae needs attention on a world level.

Stethoconus japonicus, unlike any other mirid known from North America, is distinguished from all other Nearctic genera and species by the deeply punctate, swollen pronotum, wide pronotal collar, cleft claws having simple hairlike parempodia, the cone-shaped scutellum, and the broadly rounded, shiny, partially translucent hemelytra, with a wide embolium, a large white spot on the middle of the corium, and a large, transverse, dark-brown band through the embolium, corium, and clavus (Fig. 1). As mentioned, it will key to the genus *Hyaliodes* in Slater and Baranowski (1978: 188) if the hemelytra are considered completely transparent and glassy. If this choice is not accepted, that is, if the wings are considered "somewhat glassy," then the second antennal segment must be clavate distally, which it is not. Therefore, couplet 140 in Slater and Baranowski should be modified to read as follows:

- 140 Scutellum greatly swollen, nearly cone-shaped *Stethoconus*
 140a Scutellum flattened or only slightly raised 140'
 140' Front wings almost completely transparent and glassy in appearance
 *Hyaliodes*

140" Front wings subopaque throughout or only partially transparent, if appearance somewhat glassy then antennal segment 2 abruptly clavate distally 141

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**A NEW SPECIES OF *POLYCENTROPUS*
(TRICHOPTERA: POLYCENTROPODIDAE) FROM CUBA¹**

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29634-0365.

Abstract.—*Polycentropus mathisi*, new species, is described and illustrated. It is distinct from the other nine species of the *nigriceps* species-group in the form of the preanal, intermediate, and inferior appendages and in details of the phallus.

This is the third species of the *Polycentropus nigriceps* species-group described from Cuba in this decade, bringing to four the number of species from this large island. The widely distributed *P. nigriceps* Banks, 1938, is known from mountainous areas of Pinar del Rio, Las Villas, and Oriente Provinces, while *P. criollo* Botosaneanu, 1980, is known only from the holotype collected from Pinares de Mayari, northern Oriente Province, and *P. turquino* Botosaneanu, 1980, is known from two males and a female taken from "Pico Cuba, Massif Turquino, Sierra Maestra," southern Oriente Province. The fourth species, described here, is known from one male and three females collected in Soroa, Pinar del Rio Province. In addition to the four Cuban species, four species are known from Hispaniola, one from Jamaica, and one from Puerto Rico. The systematics and biogeography of this distinct, monophyletic group of Greater Antillean caddisflies has been reviewed by Flint (1976) and Hamilton (in press).

***Polycentropus mathisi* Hamilton, NEW SPECIES**

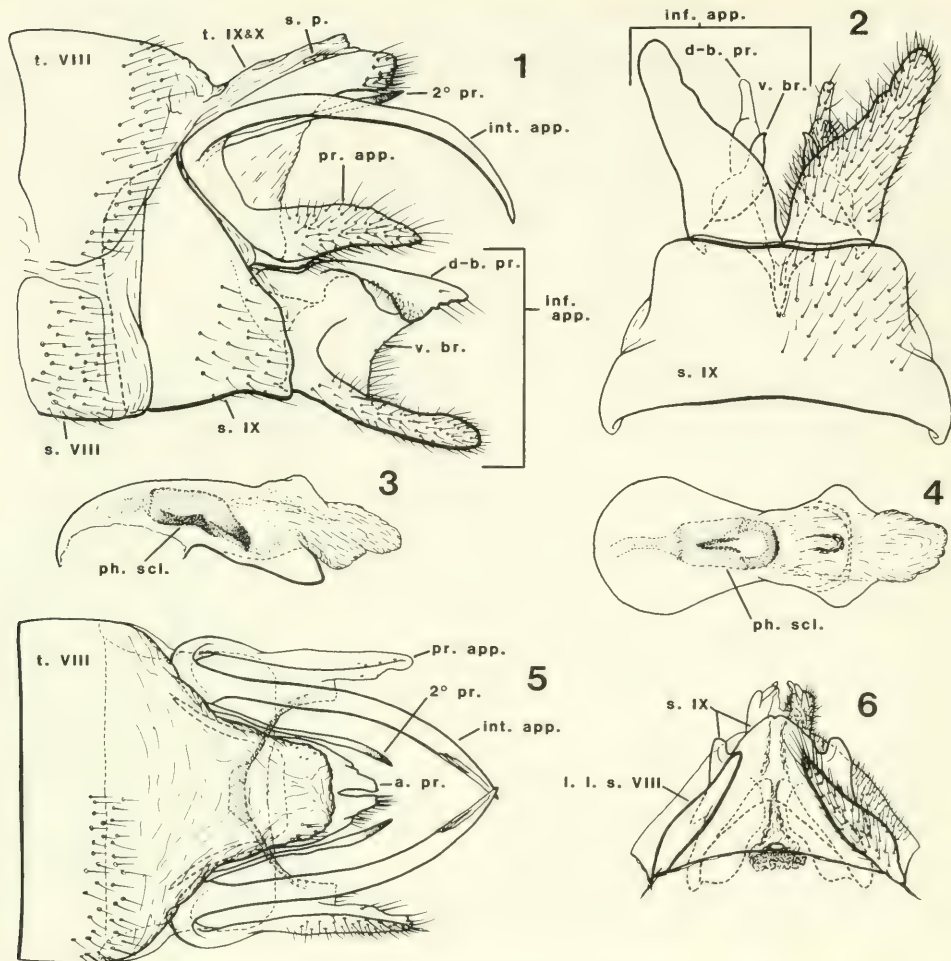
Figs. 1-6

Several characters of the male genital segments render this species distinct from all other species of the *nigriceps* group. The dorsobasal process of the inferior appendage is broadened and blade-like apically, the preanal appendage is acute and lanceolate, and the intermediate appendage bears a long, thin, weakly sclerotized secondary process which originates mesobasally. Also, the vertical brace of the inferior appendage bears a large, acute, posterior prominence.

Description.—Length of forewing: Male, 6.3 mm; female, 7.6-8.4 mm. Legs and thorax pale yellow, abdomen pale brown, dorsum of head and thorax brown; forewings dark brown, with numerous, scattered, small spots of yellow hairs; hindwing with scattered, brown setae.

Male genitalia.—Sternite IX (s. IX) angulate, anterior margin straight for most of its length, anterodorsal corner rounded, posterodorsal surface sloping from

¹ Technical Contribution No. 2534 of the South Carolina Agricultural Experiment Station, Clemson University.



Figs. 1-6. *Polycentropus mathisi*. Male terminalia, 1-5: 1, left lateral; 2, ventral; 3, phallus, left lateral; 4, phallus, dorsal; 5, dorsal. 6, Female terminalia, ventral. a. pr. = apical process, d-b. pr. = dorso basal process, inf. app. = inferior appendage, int. app. = intermediate appendage, l. l. s. VIII = lateral lobe of sternite VIII, ph. scl. = phallotremal sclerite, pr. app. = preanal appendage, 2° pr. = secondary process, s. p. = setose patch, s. VIII = sternite VIII, s. IX = sternite IX, t. VIII = tergite IX, t. IX & X = tergites IX and X, v. br. = vertical brace.

acute dorsal point to truncate posteroventral corner. Tergum IX and X (t. IX & X) lightly sclerotized ventrally with pair of broad, short, setate, apical processes (a. pr.); dorsal surface membranous with pair of slightly raised setose patches (s. p.), one on either side. Preanal appendage (pr. app.) in lateral aspect simple, narrow, acute posterad, with vestiture of fine, elongate setae; ventromesal surfaces of preanal appendages connected by narrow, sclerotized, subphallic band. Intermediate appendage (int. app.) long, narrow, evenly curved in lateral aspect, with mesal secondary process (2° pr.) originating mesally at base; secondary process thin, $\frac{2}{3}$ length of intermediate appendage, lightly sclerotized except at apex. Inferior appendage (inf. app.) with dorsobasal process (d-b. pr.) straight, apical

portion with ventral rounded point, acute apex; ventral portion of each inferior appendage linear, narrow in lateral aspect, ventral portions divergent when viewed from below, each narrowed apically; vertical brace (v. br.) of inferior appendage with prominent, acute, posterior point. Phallus with lightly sclerotized phallobase bearing dorsomesal bump, pair of apicolateral flanges, and apical pair of ventrolateral flanges; phallotremal sclerite (ph. scl.), in lateral aspect, with darkly sclerotized, beak-like distal area and dark ventral band, in dorsal aspect with distomesal opening and paired dark mesal bands before opening.

Female genitalia.—Lateral lobes of sternite VIII (l. l. s. VIII) narrow, blade-like, tapering apically. Sternite IX (s. IX) trilobate posteriorly, central lobe broad with small mesal notch; each lateral lobes somewhat truncate, narrower than central lobe. Vaginal sclerites indistinct, membranous, posteriorly, with round, mesal sclerite bearing rimmed central opening.

Type material.—*Holotype*: ♂, CUBA, Pinar del Rio Province, Soroa, 27–28.iv.1983, W. N. Mathis. *Paratypes*: 3 ♀, same data as holotype. All specimens are in the U.S. National Museum of Natural History, Washington, D.C.

Etymology.—This species is named for its collector, Wayne N. Mathis of the U.S. National Museum of Natural History.

ACKNOWLEDGMENTS

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NEOTROPICAL TINEIDAE, III: THE GEOGRAPHICAL ORIGINS
AND SYSTEMATIC RELATIONSHIPS OF TWO SPECIES
QUESTIONABLY ATTRIBUTED TO THE
AMERICAS (LEPIDOPTERA)

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Abstract.—Two species of tineid moths previously described by Edward Meyrick and considered by him as introductions into England from either North or South America are re-examined and illustrated. One of these, *Metarsiora horrealis* Meyrick is now considered a junior synonym of the southern European *Ateliotum insulare* (Rebel). On the basis of subsequently collected specimens, a Neotropical origin of the second species, *Opogona antistacta* Meyrick, is hereby confirmed. The adults and male genitalia are illustrated for both species as well as the male pupa of *O. antistacta*.

In 1937, Edward Meyrick described two species of Tineidae from unique specimens collected in London warehouses that contained imported plant material. For different reasons, Meyrick believed both specimens were introductions from either North or South America. In the course of my studies on the Neotropical Tineidae, it has been necessary to re-examine these two problematical species.

Metarsiora horrealis (Figs. 1, 3) was originally thought by Meyrick to be of the "American type" and was collected at a site where nuts from North and South America were stored. An Old World origin for the species was correctly shown by Bradley (1966: 216) when he synonymized this taxon under *Ateliotum insulare* Rebel, a species known from the Canary Islands and Sicily. Although this synonymy was repeated in the British Check List (Bradley et al., 1972), Zagulajev (1975) did not list *Metarsiora horrealis* in his revision of the Myrmecozelinae. A complete synonymy of *Ateliotum insulare* follows.

Ateliotum Zeller

Ateliotum Zeller, 1839: 189 (type species: *Ateliotum hungaricellum* Zeller, 1839).
Dysmasia Herrich-Schäffer, 1853: vol. 5: 23 (type species: *Dysmasia petrinella* Herrich-Schäffer, 1853).

Hyoprora Meyrick, 1908: 754 (type species: *Hyoprora crymodes* Meyrick, 1908).
Hylophygas Meyrick, 1932: 119 (type species: *Hylophygas convicta* Meyrick, 1932).
Saridocompsa Meyrick, 1937: 112 (type species: *Saridocompsa cypellias* Meyrick, 1937).

Metarsiora Meyrick, 1937: 76 (type species: *Metarsiora horrealis* Meyrick, 1937).



Figs. 1-2. Adults. 1, *Ateliotum insulare* (♂ holotype of *Metarsiora horrealis*), length of forewing 4.8 mm. 2, *Opogona antistacta*, ♂ holotype, length of forewing 6.2 mm.

***Ateliotum insulare* (Rebel)**

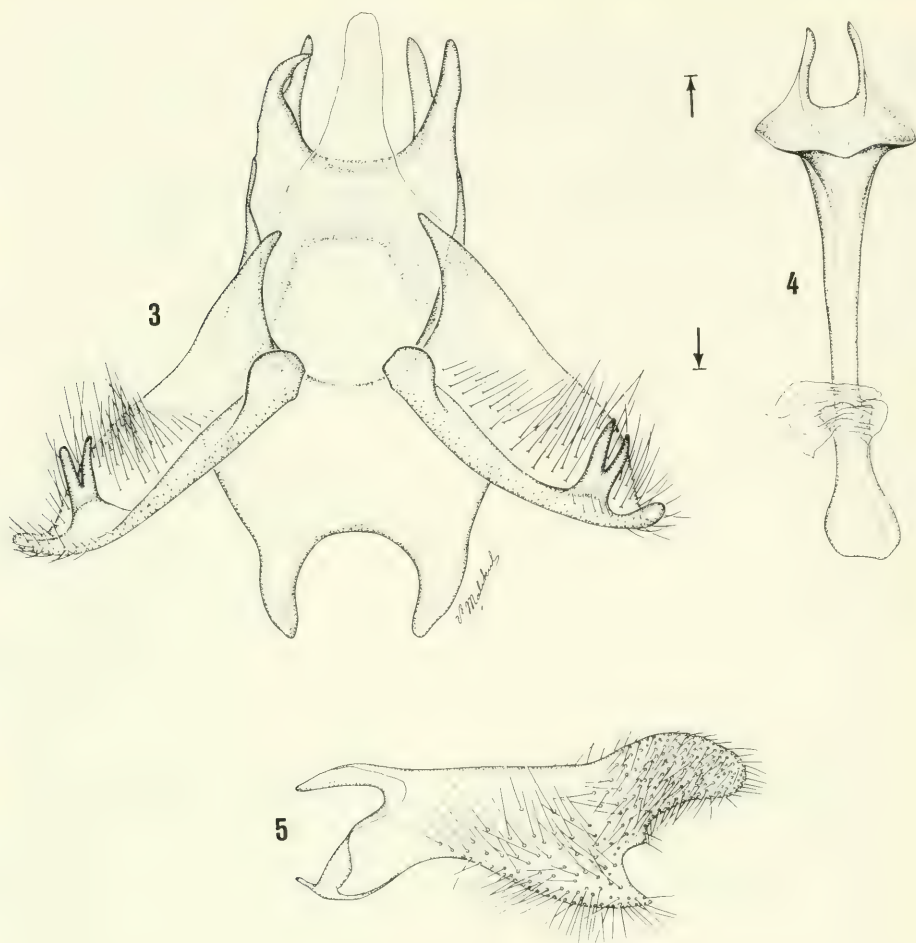
Figs. 1, 3-4

Dysmasia insularis Rebel, 1896: 125.—Rebel in Standinger and Rebel, 1901 (pt. 2): 241.—Caradja, 1920: 172.

Ateliotum insulare (Rebel).—Petersen, 1957: 561.—Zagulajev, 1975: 229.

Ateliotum insularis (Rebel).—Bradley, 1966: 216.—Bradley, Fletcher, and Whalley, 1972: 7.

Metarsiora horrealis Meyrick, 1937: 76.—Bradley, 1966: 216 (synonym of *Ateliotum insulare* (Rebel)).—Bradley, Fletcher, and Whalley, 1972: 7.



Figs. 3-5. Male genitalia. 3, *Ateliotum insulare*, ventral view, scale = 0.25 mm. 4, Same, aedeagus. 5, *Opogona antistacta*, lateral view of valva.

A few corrections should be noted in Meyrick's description of *M. horrealis*. An antennal pecten consisting of at least 4-6 brown hairs is present in contrast to his statement that a pecten is absent. Similarly, he reports the haustellum absent which should be checked in a cleared specimen, because Zagulajev (1975: fig. 127) shows both a reduced haustellum and maxillary palpus present in *Ateliotum hungaricellum* Zeller. Meyrick also stated that all veins are present in the forewing when in fact one radial vein is lacking as shown by Zagulajev (1975: fig. 151a).

Opogona antistacta Meyrick

Figs. 2, 5-11

Opogona antistacta Meyrick, 1937: 87.

Opogona antistacta was reared from a larva found in London feeding under a slight tubular web on banana rind. The unique male holotype is lacking an abdomen, which has cast some uncertainty on its identity. One key feature in the

forewing pattern of the holotype is the presence of a pair of small subapical fuscous spots (Fig. 2) which are also present in three male specimens believed originally from the circum-Caribbean area. Two were intercepted at ports in the United States (Baltimore and Philadelphia), with one specimen suspected to have originated from Colombia and the other from Cuba (on banana rubbish). A third specimen was collected and reared in Cuba on sugar cane. The genitalia of all three are identical. Because this species is now believed to be indigenous to the Neotropical region and its identity previously in doubt, a full description is warranted.

Adult (Fig. 2).—Length of forewing: ♂ 4–6.2 mm. A small, buff to light brown moth with a pair of minute, rather faint, fuscous subapical spots, one on costa and the other approximately opposite on termen. Female unknown.

Head: Vestiture smooth; scales of vertex light brown, projected forward as a round ridge extending between antennal bases; scales darker brown posterior to ridge; frons beneath vertex ridge with a double row of white scales forming a skirt-like fringe above mouthparts. Antenna approximately 0.8 the length of forewing, 70-segmented; scape smooth, elongate and slightly depressed, light brown, pecten absent; flagellum smooth, light brown streaked with fuscous; a single row of scales completely encircling each segment; ventral sensory setae reduced. Maxillary palpus moderately short, not extending to apex of labial palpus II, buff to cream; haustellum reduced, slightly exceeding length of maxillary palpus. Labial palpus 3-segmented, elongate, dark brown laterally, cream ventrally; 4–5 slender buff hairs arising laterally from segment II; apical segment relatively broad and flat.

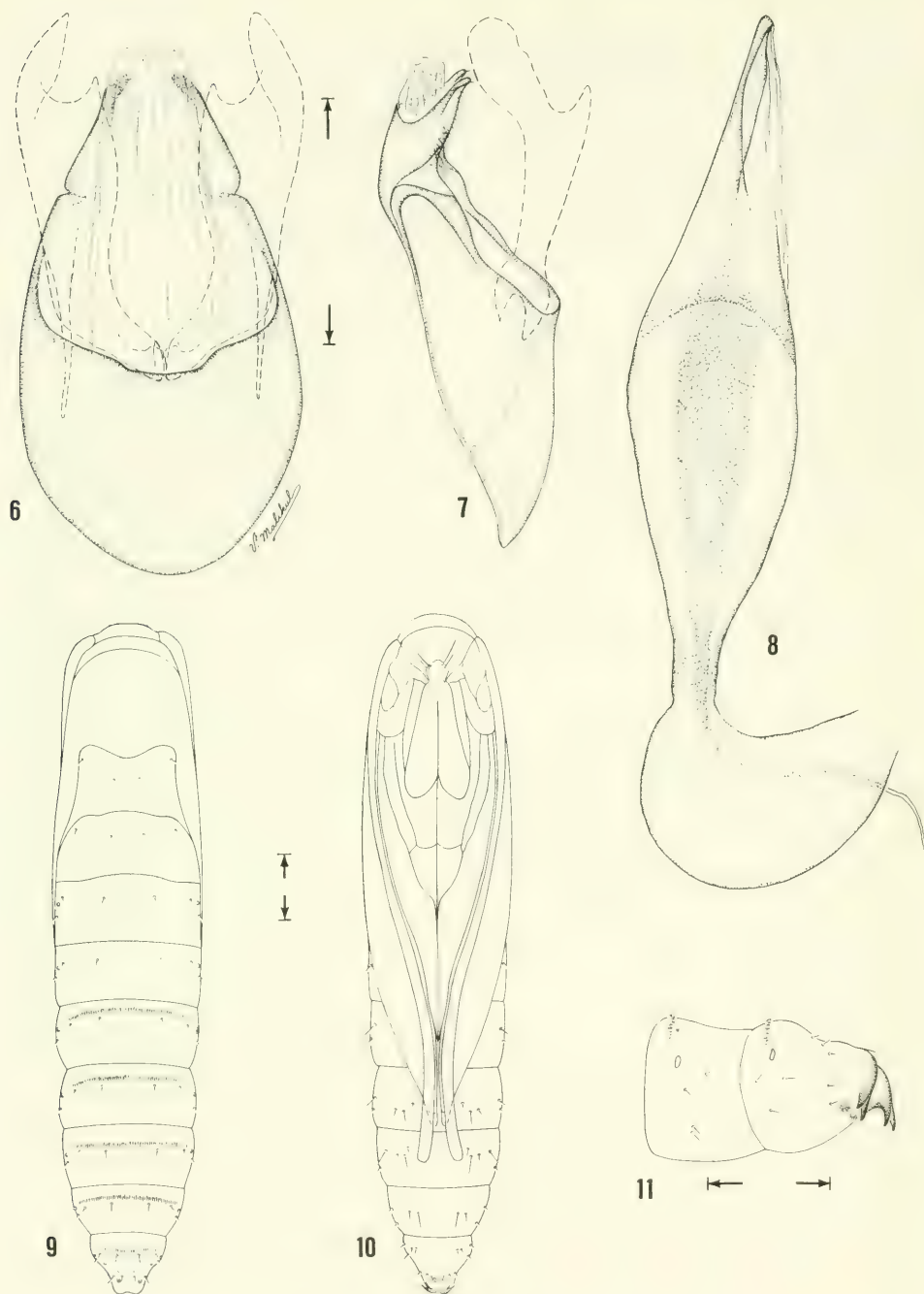
Thorax: Pronotum light brown. Venter silvery white to cream. Forewings mostly light brown with suffusion of darker brown scales over distal two thirds; a small, rather indistinct fuscous spot at subapex of costa; a similar even smaller spot present at same level on subapex of termen; fringe consisting of very fine buff hairs. Hindwing uniformly pale buff with a slight golden luster; fringe elongate, approximately twice the greatest width of wing. Foreleg cream to buff ventrally, dark fuscous dorsally with apices of tibia and tarsal segments ringed with buff. Midleg similarly marked as foreleg but generally paler and irrorated with buff dorsally. Hindleg uniformly buff to cream.

Abdomen: Light brown dorsally, cream to pale buff ventrally.

Male genitalia: As shown in Figs. 5–8. Uncus fused to tegumen, bifid with lobes widely separated and only slightly setigerous. Tegumen a moderately narrow band dorsally. Vinculum long and broad, with anterior margin broadly rounded. Valva constricted near base, then becoming gradually wider toward broadly excavated outer margin; ventral margin of valva produced into a sharp lobe. Aedeagus elongate conical, with a grooved apex; cornuti absent.

Larva.—Unknown.

Male pupa (Figs. 9–11).—Length 5.5 mm; maximum width 1.3 mm. Color (dried exuvium) light brown. Head round, with reduced frontal process (cocoon cutter). Labial palpus elongate, extending nearly to T3; caudal end broadened. Forewing extending to A5. Antenna to middle of A5. A single anterior row of minute dorsal spines present on A3–7; tabulation of dorsal spines as follows: A3 = 67, A4 = 64, A5 = 65, A6 = 62, A7 = 57. Cremaster composed of a pair of stout, bifurcate, ventral spines from end of terminal segment. Caudal spines absent from dorsum of A8 + 10.



Figs. 6-11. *Opogona antistacta*. 6, Male genitalia, ventral view, scale = 0.25 mm. 7, Lateral view. 8, Aedeagus. 9, Male pupa, dorsal view, scale = 0.5 mm. 10, Dorsal view. 11, Caudal end with cremaster, lateral view, scale = 0.5 mm.

The pupal illustration is a reconstruction of the shell after adult emergence. Consequently, I am uncertain as to the precise shape of the vertex. Because few pupae of *Opogona* have been illustrated, I am also uncertain of the diagnostic features of this stage. Comparisons with that figured for *O. omoscopa* Meyrick (Davis, 1978: 18) show the structure of the cremaster to differ greatly. In *O. antistacta*, the cremaster is ventral (versus dorsal in *omoscopa*) and consists of two sets of spines (versus simple).

Holotype.—♂, BMNH.

Type locality.—London, England [presumed imported from Latin America].

Distribution.—Probably circum-Caribbean. This species is apparently a minor pest on stored plant material, especially banana and sugarcane.

Material examined.—4 ♂ and 1 ♂ pupa. ENGLAND: London: 1 ♂ (holotype), 8 Sept. 1936, S. Wakely (BMNH). CUBA: Camaquey Prov.: Central Jaronú: 1 ♂ with pupal exuvium, 5 May 1927 (USNM). UNITED STATES: Maryland: Baltimore [intercepted on a ship from Colombia]: 1 ♂, Jan. 1936 (USNM). Pennsylvania: Philadelphia [intercepted on banana refuse from Cuba]: 1 ♂, 21 May 1928 (USNM).

ACKNOWLEDGMENTS

I thank G. Robinson and K. Tuck (BMNH) for the loan of type specimens. My assistant, V. Malikul, prepared the line drawings, and V. Krantz of the Smithsonian Photographic Laboratory is responsible for the photographs. Silver West of our Department typed the final draft of the manuscript.

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THREE CUCKOO WASPS FROM SIBERIAN AND BALTIC AMBER (HYMENOPTERA: CHRYSIDIDAE: AMISEGINAE AND ELAMPINAE)

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Abstract.—*Protamisega khatanga* Evans (Amiseginae) from Siberian amber is redescribed. *Protadelphe aenea* (Amiseginae) and *Palaeochrum diversum* (Elampinae), both new genera and species, are described from Baltic amber. *Omalus primordialis* Brues is assigned questionably to *Palaeochrum*.

A. P. Rasnitsyn, Palaeontological Institute, USSR Academy of Sciences, Moscow, invited me to study and describe two fossil Chrysididae from Baltic amber. The present opportunity is taken to redescribe *Protamisega khatanga* Evans from Siberian amber and to comment on the position of *Omalus primordialis* Brues. The specimens were studied in immersion oil having a similar refractive index to that of the amber.

Subfamily Amiseginae

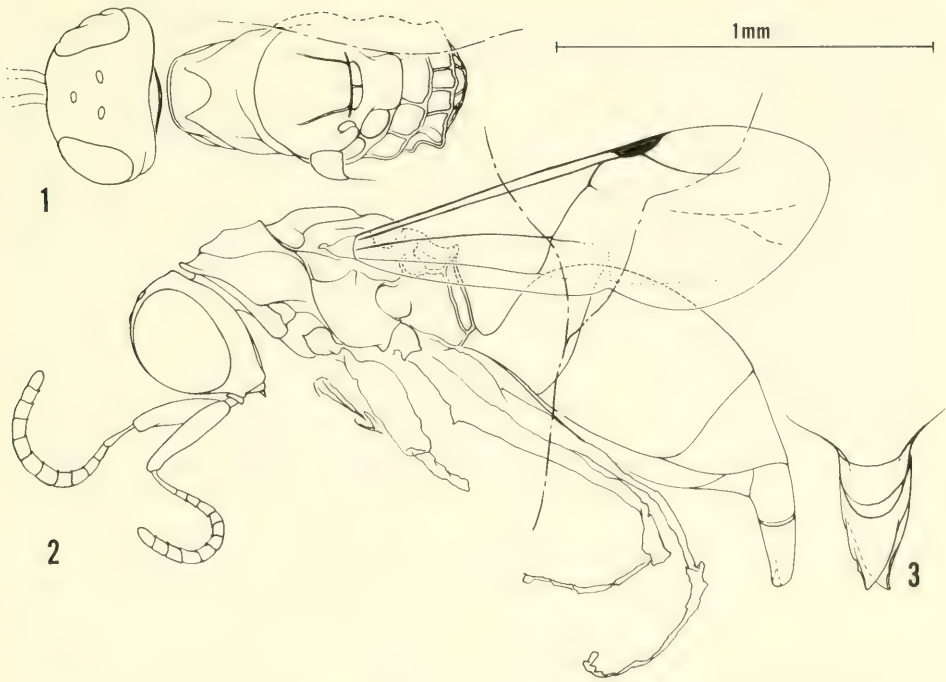
The Amiseginae is a tropicopolitan group. The fossil record is scanty, the only known genera being *Protamisega* Evans from Siberian amber of Upper Cretaceous age and *Protadelphe*, new genus, from Baltic amber of Upper Eocene age. Both areas of what is now northern Eurasia had a warm tropical climate during those ages. Recent Amiseginae maintain an essentially tropical habitat with outliers in Mexico, southern United States, China, Japan, southeastern Australia and southeastern Africa exclusive of Madagascar.

Hosts are known for four genera and nine species of Amiseginae (Krombein, 1983: 8). All were reared from walking stick eggs (Phasmatodea). The similarly shaped, sharply pointed mandibles in females of all recent amisegines is presumptive evidence that all recent genera parasitize such eggs, for the mandibles are adapted to pierce the tough cuticle of the egg for feeding and oviposition. Regrettably, no such presumption can be made for the fossil genera. *Protamisega* is a male and the oral area in the *Protadelphe* female is obscured by an opaque milky inclusion (mold or regurgitated material). The latter genus, however, is so closely related to *Adelphe* Mocsary, that such a host relationship is likely. The earliest phasmatid fossils are Paleocene (Sharov, 1971: 121), so phasmatids would have been available as hosts when *Protadelphe* was active.

Protamisega khatanga Evans

Figs. 1-3

The genus and species were described from a unique specimen in Baltic amber of Upper Cretaceous age from Taimyr Peninsula, North Siberia (Evans, 1973:



Figs. 1–3. *Protamisega khatanga*. 1, Head and thorax (dorsal view). 2, Habitus (lateral view; Y across base of abdomen denotes fracture lines). 3, Apex of abdomen (ventral view).

176–177, figs. 9–10). The specimen is somewhat distorted and some details are difficult to ascertain.

Male.—Head and thorax dark brown, abdomen lighter brown, appendages quite pale, giving overall appearance of some decolorization; no visible vestiture. Length 2.0 mm, forewing 1.3 mm.

Head: Dorsal and lateral views (Figs. 1, 2); eyes moderately bulging, ocular setae not visible at $150\times$, height two-thirds head width; antenna 13-segmented, pedicel longer than first flagellar segment, first and second flagellar segments subequal in length; front of head not visible; mandible largely obscured but apex with sharp point; malar space not grooved.

Thorax: Dorsal and lateral views (Figs. 1, 2); pronotum moderately long, without lateral lobe, not extending to tegula, anteriorly with transverse carina that curves toward midline, without median groove or fovea; notauli diverging anteriorly but not reaching anterior margin of scutum; scutellum twice as long as metanotum, anteriorly with transverse median groove divided by longitudinal carina; metanotum raised slightly above level of propodeum; propodeum short dorsally, transversely carinate posteriorly, surface with several longitudinal carinae delimiting a series of foveae, posterolaterally obtusely angulate; posterior propodeal surface abruptly declivous, apparently with several carinae radiating outward from area of abdominal attachment; lateral thoracic sculpture obscure; forewing as figured; legs rather distorted, tarsal claws possibly simple.

Abdomen: Lateral view (Fig. 2), terminal segments in ventral view (Fig. 3); four normally exposed segments, terminal segments exerted to form a tapering tele-

scoped tube in lateral view; male terminalia visible in ventral view with compound microscopy but detailed structure not resolvable.

Female.—Unknown.

Type-depository.—Palaeontological Institute, USSR Academy of Sciences, Moscow, No. 3130-19.

Discussion.—The discovery that the specimen is a male, not a female as believed earlier, explains the apparent anomaly of the decidedly unfeminine antennae. Amisegine females have an elongate first flagellar segment that is substantially longer than either the pedicel or second flagellar segment (cf. Fig. 5). *Protamisega* has the first and second segments short and subequal in length.

The anterior scutellar groove of *Protamisega* is unique among the Amiseginae. A similar groove, however, or modifications in the form of a pair of anterolateral pits, is a common feature in many genera of Bethyilidae.

The relatively short metanotum suggests that *Protamisega* is closer to the more primitive New World genera of Amiseginae and to the recently described African *Anachrysis* (Krombein, 1986) than to the more highly specialized Australasian or African series of genera. *Protamisega* has no close affinity to *Anachrysis* or to the New World *Amisega* Cameron, *Mesitiopterus* Ashmead and *Microsega* Krombein. The latter four genera have the dorsal surface of the propodeum rounding gradually into the lateral and posterior surfaces and not angulate posterolaterally.

Males of the New World *Adelphe* Mocsary and *Duckeia* Costa Lima have a relatively short metanotum and also possess dentate posterolateral angles of the propodeal dorsum. Both genera differ from *Protamisega* in having a malar groove and parapsidal furrows, and lack the transverse series of propodeal foveae. *Duckeia* lacks an occipital carina; it also lacks an anterior carina on the pronotal disk, and has a median groove on the pronotum. *Adelphe* has an anterior carina on the pronotal disk as well as an occipital carina. I do not regard either of these recent genera as particularly close to *Protamisega*. The Eocene *Protadelphe* described below perhaps is closer to the Cretaceous *Protamisega* but has already diverged considerably by developing a malar groove, an occipital carina, a much better defined pronotal lobe, a posteromedian fovea on the pronotum, the loss of the anterior scutellar groove, and the metanotum at the same level as the propodeum.

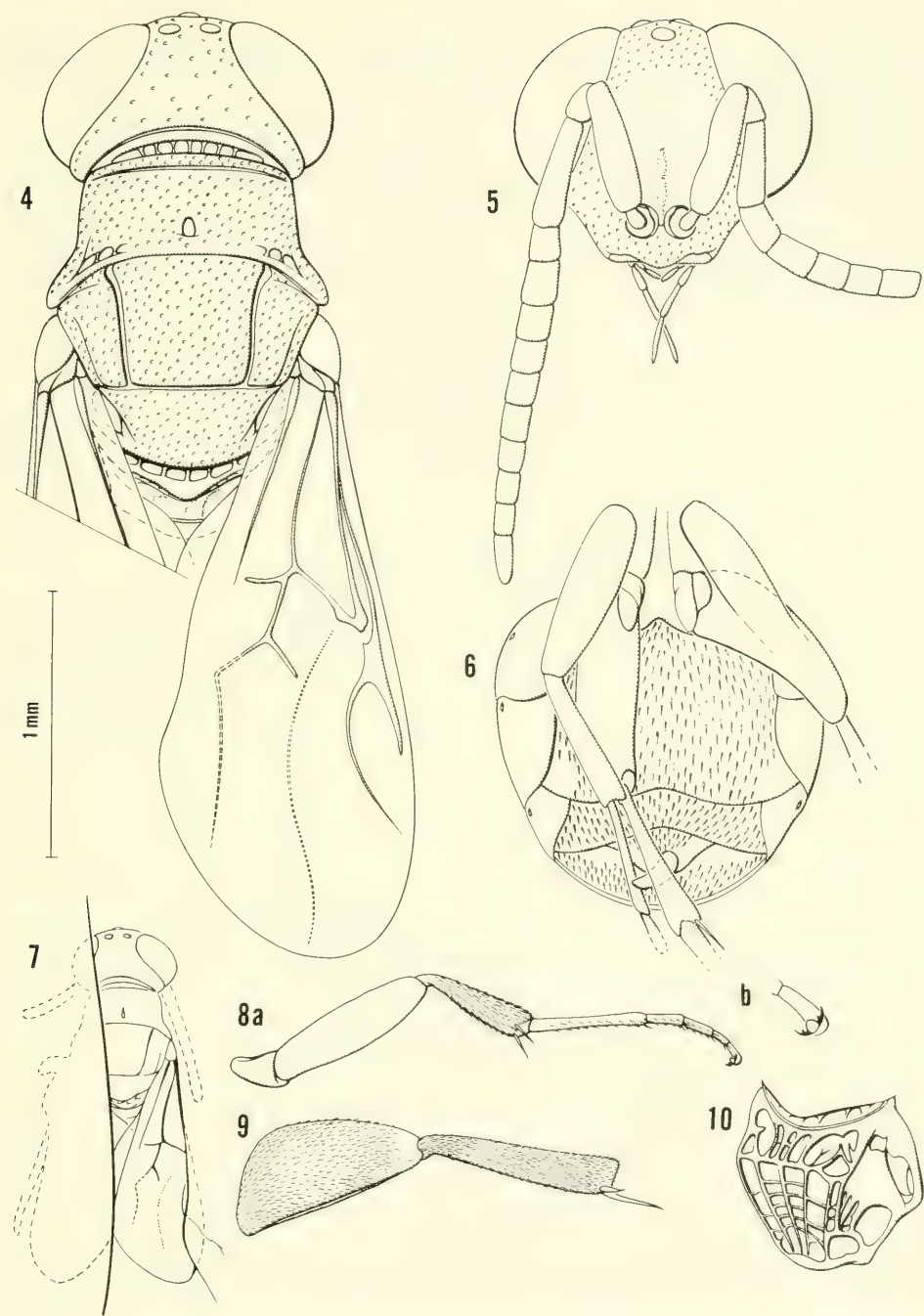
Protadelphe Krombein, NEW GENUS

Type-species.—*Protadelphe aenea* Krombein, new species.

Etymology.—The generic name is feminine and is derived from the Greek *protos*, first, and *adelphe*, sister.

Female.—Small, fully winged, relatively stocky amisegine.

Head: Dorsal and frontal views (Figs. 4, 5); apex of mandible not visible; malar areas strongly convergent below, about half as long as eye height, with groove from lower eye margin toward mandible; scapal basin moderately concave, smooth; eye moderately bulging, converging strongly above, ocular setae not visible at 150×; ocelli small, set in compact triangle, hind ocelli separated from each other by about diameter of ocellus, lateral ocellar distance half that; occipital carina well-developed but not margined by anterior crenulate groove; vertex without median ridge; antenna 13-segmented; flagellar segments 2–6 with flattened sensory areas beneath (cf. Krombein, 1983: 71, figs. 41 et seq.), venter of segments 7–11 not visible.



Figs. 4–10. *Protadelphe aenea*. 4, Head, thorax and right forewing (dorsal view). 5, Head (frontal view). 6, Abdomen and part of legs (ventral view). 7, Habitus (dorsal view of part clearly visible, reduced). 8a, Midleg except coxa. 8b, Tarsal claws of midleg (enlarged). 9, Hind femur and tibia. 10, Propodeum (right oblique aspect from above).

Thorax: Dorsal view (Fig. 4); pronotal collar with transverse row of foveae, disk carinate anteriorly but not laterally, posteriorly with small median pit, lobe almost attaining tegula; scutum with notauli complete, curved outward on anterior third, parapsidal line present on apical two-thirds; scutellum two-thirds as long as scutum; metanotum a third as long as scutellum, transversely foveate at base, not raised above level of propodeum; mesopleuron not carinate anteriorly; right oblique aspect of propodeum from above (Fig. 10); dorsal propodeal surface short, with some quadrilateral foveae of irregular size, slightly angulate posterolaterally; posterior propodeal surface with several carinae radiating outward from abdominal attachment, divided into foveae of irregular size by transverse carinae; lateral propodeal surface mostly smooth but with some irregular foveae posteriorly; mid- and hind legs (Figs. 8, 9); mid coxae slightly separated; femora beneath with scattered longer setae occasionally visible; hind femur robust; tibial spurs 1-2-2; tarsal segments with two rows of tiny spines beneath; tarsal claw (Fig. 8b) with small erect tooth; forewing (Fig. 4), membrane moderately setose, Cu and m-cu nebulous but deeply stained.

Abdomen: Ventral view (Fig. 6), dorsal aspect concealed by wings; four normally exposed segments, telescoped apical section of ovipositor extruded.

Male.—Unknown.

Discussion.—*Protadelphe* is clearly a precursor of *Adelphe* in that particular amesegine lineage. Important developments in *Adelphe* are the relatively long ocular setae visible as low as $8\times$, the wider dispersion of the ocelli, the crenulate groove on the vertex anterior to the occipital carina, the extension of the anterior pronotal carina along the sides, the lack of a posteromedian pronotal fovea, and the development of an anterior carina on the mesopleural disk.

Protadelphe aenea Krombein, NEW SPECIES

Figs. 4–10

Female.—Length 3.4 mm, forewing 2.2 mm. Head and thorax with bronze reflections, abdominal integument not visible; scape, much of flagellum, femora, fore and mid tibiae and all of fore and mid tarsi light beneath, probably reddish in life. Wings hyaline, somewhat infumated in marginal and submarginal cells, costa and stigma dark brown, other veins red. Vestiture short, suberect, sparser on head than on thoracic dorsum and abdominal venter.

Head: Height 0.8 times width and 1.4 times eye height; least interocular distance 0.3 times head width; clypeus with rounded median lobe, narrow emargination between lobe and lateral area, apex not thickened; antennal scape slightly shorter than combined lengths of pedicel and first flagellar segment, the latter about as long as next three segments combined; clypeus and front with small separated punctures, vertexal punctures even more scattered.

Thorax: Dorsum of pronotum, scutum and scutellum with small punctures mostly separated by two to three times diameter of a puncture.

Abdomen: Punctures of venter small and presumably as close as on thoracic dorsum as indicated by the fungus-encrusted setae.

Type-locality and -depository.—Recent beach of Gdansk Gulf, Poland, Janina Chociwska; redeposited from the “Blaue Erde” of Upper Eocene, Sambian Peninsula west of Kaliningrad, USSR. Museum of the Earth, Warsaw, Poland, No. 6473.

Note.—This unique specimen is quite well preserved in an irregular piece of amber. There is a white deposit, perhaps due to regurgitation, in the mandibular area that extends upward as a thin coating on the lower front, obscuring the frontoclypeal suture but not the punctuation of that area. The abdomen, area between the coxae, and small areas of the pronotum are coated with a feltlike fungus that obscures the abdominal integument and extends onto the sternal vestiture causing it to appear like small prickles rather than fine setae. Polishing compound that had been used to prepare the specimen infiltrated along hairline fractures, causing opacity of the right forewing and concealing the hindwing and abdominal dorsum.

Subfamily Elampinae

Recent Elampinae occur in all of the major zoogeographic regions, but the fossil record is scanty. Recent members of the subfamily parasitize a wide spectrum of wasps and bees with diverse nesting habits including those nesting in the ground or in cavities in wood.

Palaeochrum Krombein, NEW GENUS

Type-species.—*Palaeochrum diversum* Krombein, new species.

Etymology.—The generic name is neuter and is derived from the Greek *palaaios*, ancient and *chroma*, color of the skin (as in *Hedychrum*).

Male.—Small, densely and finely punctate elampine with four normally exposed abdominal segments.

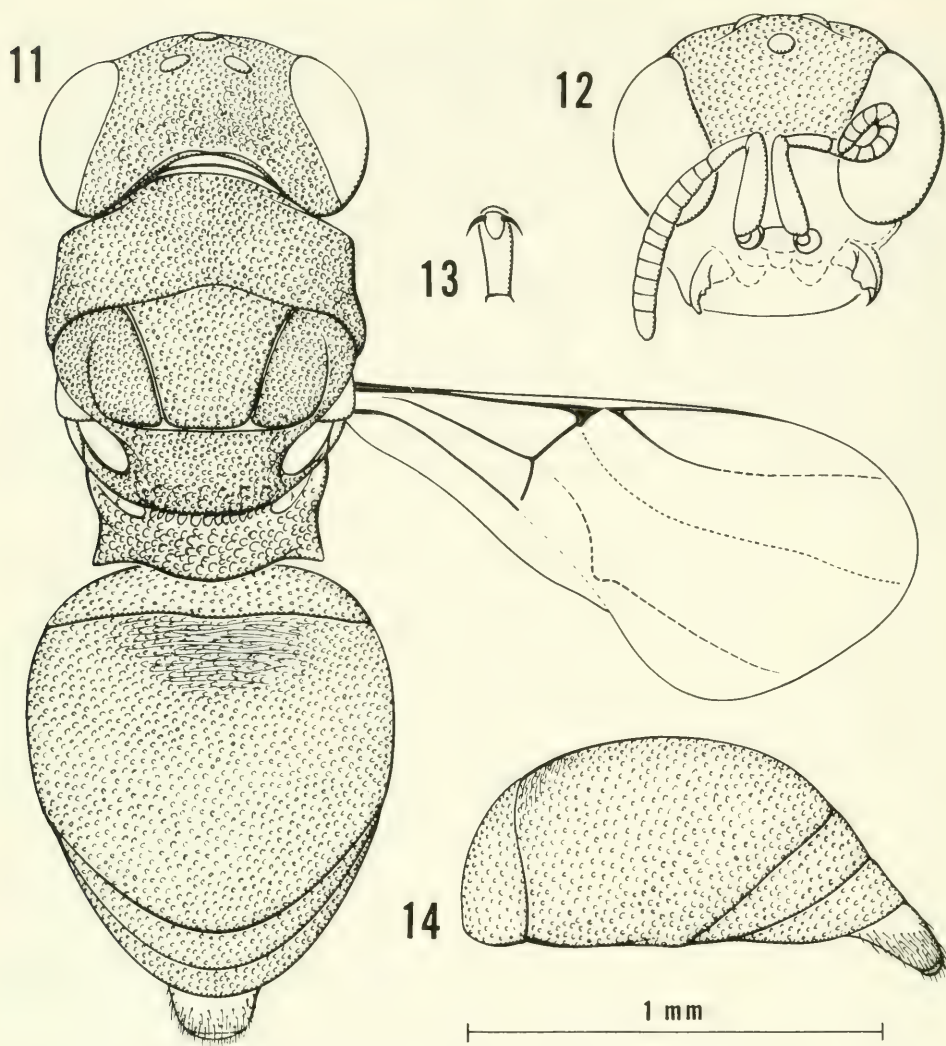
Head: Dorsal and frontal views (Figs. 11, 12), much of oral region and lower front obscured by flocculent exudate; mandibles protruding beyond flocculus, tridentate apically, outermost tooth longer; apex of clypeus apparently trilobed; scapal basin obscured; head width almost twice eye height; ocular setae not visible at 150 $\times$; genal carina strong, margined anteriorly by crenulate groove; occipital carina absent; antenna 13-segmented.

Thorax: Dorsal view (Fig. 11); mesopleuron not carinate anteriorly or produced forward; propodeum with short posterolateral angles; venation of forewing difficult to resolve due to hairline fracture that admitted air, but stigma small, marginal cell almost closed but apical section may be nebulous, discoidal cell lacking; tibial spurs 1-2-2; tarsal claws simple (Fig. 13).

Abdomen: Dorsal and lateral views (Figs. 11, 14); segments 1–4 normally exposed, with metallic coloration; 5 and apex of 6 exserted, not metallic; sternum slightly concave.

Discussion.—*Palaeochrum* is unique in having four, rather than the normal three, exposed abdominal segments with metallic coloration. The fifth and sixth segments are visible but are brown, non-metallic, and undoubtedly were exserted during the insect's efforts to extricate itself from the resin. An unusual feature is the simple tarsal claw. All recent elampines have one or more teeth on the inner edge of the claw except *Xerochrum* Bohart of the southwestern deserts in North America and *Prochridium* Linsenmaier from similar habitats in Egypt and Turkmen SSR. *Palaeochrum* has the general habitus of *Hedychridium* Abeille de Perrin which, however, has only three normally exposed abdominal segments, spinose posterolateral propodeal angles, and a toothed tarsal claw.

I assign *Omalus primordialis* Brues (1933: 153–154, figs. 83, 84) to *Palaeochrum*



Figs. 11–14. *Palaeochrum diversum*. 11, Habitus (dorsal view; appendages lacking except right forewing). 12, Head (frontal view). 13, Tarsal claws. 14, Abdomen (lateral view).

with some question. It was described from two females from Baltic amber attributed to the Oligocene in the Königsberg museum. Part of that amber collection was lost during World War II and part of it is now in Göttingen University, West Germany. Brues' type series is not in Göttingen so it must be presumed lost. His figures show a species having the habitus of *Palaeochrum* but with three abdominal segments; his description says "four tergites and an extremely short fifth." He could not ascertain the form of the tarsal claws but stated that the scapal basin was transversely ridged or striate. Brues described his species as black with no metallic reflections. It is unlikely that *primordialis* is conspecific with the metallic green *diversum* unless there was a post-mortem color change in the former species due to hydration.

Palaeochrum diversum Krombein, NEW SPECIES

Figs. 11–14

Male.—Length 2.3 mm, forewing 1.4 mm. Integument metallic green; tibiae, tarsi and abdominal segments 5–6 brown. Wings hyaline, stigma and veins dark brown. Vestiture short, inconspicuous, appressed on terga.

Head: Closely punctate becoming somewhat pitted on vertex; least interocular distance 0.37 times head width and 0.7 times interocular distance at posterior ocelli.

Thorax: Dorsum with close fine punctures; mesopleuron with larger contiguous pits; propodeum with smaller contiguous pits.

Abdomen: Dorsum polished, with small punctures mostly separated by slightly more than a puncture's width; second tergum anteriorly with small median area bearing fine close transverse carinae with interspersed small punctures; terminalia not visible.

Female.—Unknown.

Type-locality and -depository.—Gdansk-Skogie, Poland, Holocene fossil beach sediments, depth 12 or more meters, Tadeusz Gieciwicz; redeposited from the "Blaue Erde" of Upper Eocene, Sambian Peninsula west of Kaliningrad, USSR. Museum of the Earth, Warsaw, Poland, No. 19774.

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INSECTS ASSOCIATED WITH PURPLE LOOSESTRIFE
(*LYTHRUM SALICARIA* L.) IN EUROPE

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Abstract.—In Europe, 120 species of phytophagous insects, including 14 species apparently restricted to *Lythrum*, and 64 species of floral visitors were found associated with purple loosestrife, *L. salicaria* L. Of potential value for the biological control of this aggressive alien weed in North American wetlands are: *Dasineura salicariae* (Cecidomyiidae); *Hylobius transversovittatus*, *Nanophyes marmoratus*, *N. brevis* (Curculionidae); *Pyrrhalta californiensis*, *P. pusilla*, *Aphthona lutescens*, *Altica lythri* (Chrysomelidae); and *Acleris lorquiniana* (Tortricidae). Ecological, bionomic, and host-specificity investigations of these natural enemies are needed.

Purple loosestrife, *Lythrum salicaria* L. (Lythraceae), is considered by some ecologists to be a menace to our North American wetlands because it displaces native wildlife foods such as cattails (*Typha* spp.). Control by chemical or mechanical methods is difficult and usually not practical for large, well-established stands (Stuckey, 1980). For these reasons, and because biological control is compatible with wildlife conservation and management in wetlands, a search for natural enemies of purple loosestrife in Europe was undertaken. However, because ornamental purple loosestrife is widely cultivated, garden escapes are common (Stuckey, 1980), and beekeepers may propagate it as a nectar source (Pellett, 1966). These uses pose conflicts of interest regarding the feasibility of biological control.

This tall, vigorous, herbaceous perennial is native to Eurasia and usually found in freshwater wetland habitats (Hultén, 1971; Stuckey, 1980). In mid- to late summer, it bears three types of self-incompatible, insect-pollinated, vivid magenta flowers that are densely packed throughout conspicuous vertical verticillate spikes (Levin and Kerster, 1973; Teale, 1982). Each plant may bear as many as 3000 flowers, yielding 300,000 seeds; a pure stand of purple loosestrife may thus produce up to 59 billion seeds per hectare (24 billion/acre; Teale, 1982).

In Europe, purple loosestrife may occasionally form dense monospecific stands, on calcareous or acid soils (Shamsi and Whitehead, 1974), but it usually occurs as a minor component (1-4% of cover) of mixed wetland vegetation (Bodrogozzy

and Horvath, 1977). In North America, purple loosestrife was first recorded from New England and southeastern Canada in 1814 (Stuckey, 1980). Subsequently it spread to 33 states, with the largest populations in the formerly glaciated portions of the northeastern and Great Lakes states (Stuckey, 1980). The minute seeds of this aggressive plant are usually water-borne, but they may be disseminated by wildlife and livestock. Plants can also regenerate from stem or rootstock fragments.

MATERIALS AND METHODS

Field surveys for insects were made in July–August 1979 (Batra); September–November 1980 (Boldt); and May–August 1981 (Mendl, Batra) at 13 sites in Emilia Romagna, Lombardia, Umbria, Calabria, Sicilia, Sardegna, Piemonte, Veneto and Lazio, Italy; 15 sites in Steiermark, Burgenland, and Niederosterreich, Austria; 1 site in Buskerud, Norway; 1 site in Kalmar, Sweden; and 2 sites in Croatia, Yugoslavia; some of these sites were visited repeatedly during several months. At most locations, the plants grew as scattered individuals or small clumps among mixed wetland vegetation; occasional plants also grew in dry meadows. Insects on the plants were observed, then hand-picked, aspirated, or netted and any feeding damage was noted. Living insects and immatures were placed on caged bouquets of cut stems, leaves, and flowers to assess feeding habits; immatures were reared to adulthood, when possible. Large quantities of cut or uprooted plants were bagged and brought to the laboratory and either dissected to reveal internal feeders, or caged for several weeks for the transformation and emergence of these and other cryptic insects.

RESULTS AND DISCUSSION

In Europe, 120 species of phytophagous insects were found, including 14 probably restricted to *Lythrum* spp. (Table 1); 64 species of flower visitors were also collected from purple loosestrife (Table 2). Only a few of the phytophagous species are sufficiently host-specific to be worthy of further consideration and testing for use in classical biological control (Batra, 1982).

The most promising for testing include several species of *Nanophyes* weevils that attack only *Lythrum* species, e.g. *N. annulatus* and *N. circumscriptus* galling leaves, petioles and stems, *N. globiformis* and *N. helveticus* galling stems; *N. marmoratus* and *N. brevis* mining ovaries and seeds. *Nanophyes brevis*, *N. helveticus*, and *N. circumscriptus* are restricted to *L. salicaria*, according to Dieckmann (1963). Furthermore, *N. circumscriptus* tolerates a cold climate (Kontuniemi, 1943) such as would be encountered where purple loosestrife is most abundant in North America. A related species, *Nanophyes* sp. nr. *nigritulus* attacks fruits of the aquatic weed, *Jussiaea repens*, and has been considered for use in biological control (Sankaran and Krishna, 1967). We found during our surveys that univoltine *N. marmoratus* (Fig. 2) is by far the most abundant and widespread of the genus, and it is one of the more common of all phytophages on *L. salicaria*. This weevil destroyed up to 69% of the ovules of some plants.

The multivoltine chrysomelids, *Pyrrhalta californiensis* (Fig. 3) and *P. pusilla* appear to be specific to *Lythrum* and are patchily abundant in Italy, Austria, and Yugoslavia, where dense populations on some plants cause significant (ca. 50%) defoliation. There are four generations of *P. californiensis* annually in northern Italy (Zocchi, 1953).

Table 1. Phytophagous insects associated with *Lythrum salicaria*. Legend: L, leaves; St, stems; R, roots or rhizomes; F, flowers; S, seeds. * Indicates species of greatest apparent host-specificity and potential as agents for classical biological control in North America.

Taxon	Location	Plant Part	Recorder/Remarks
Coleoptera			
Cantharidae			
<i>Rhagonycha fulva</i> (Scopoli)	E. Austria	L	Batra
Chrysomelidae			
<i>Altica ampelophaga</i> Guérin	N. Italy, E. Austria	L	Boldt; Mendl; <i>Epilobium</i> usual host, Freude et al., 1966; Phillips, 1977
<i>Altica impressicollis</i> Reiche	Sardinia, Sicily	L	Boldt
* <i>Altica lythri</i> Aubé	N. Italy	L	Boldt
<i>Altica oleracea</i> (L.)	S. Italy	L	Boldt
<i>Altica palustris</i> Weise	E. Austria	L	Mendl; <i>Epilobium</i> usual host, Freude et al., 1966
* <i>Aphthona lutescens</i> (Gyllenhal)	E. Austria, N. Italy	R, L	Batra; Boldt; Freude et al., 1966
<i>Chrysolina herbacea menthastris</i> Suffrian	Italy	L	Boldt
<i>Cryptocephalus ocellatus</i> Drapiez	E. Austria, N. Yugoslavia	L	Batra, reared
<i>Dlochrysa fastusa</i> (Scopoli)	Italy	L	Boldt
Galerucine sp.	Austria	L	Batra, reared
<i>Longitarsus</i> nr. <i>luridus</i> (Scopoli)	E. Austria	L	Batra
<i>Longitarsus tabidus</i> (F.)	N. Yugoslavia	L	Batra
* <i>Lythrarina salicariae</i> (Paykull)	Italy	L	Boldt
<i>Oulema melanopus</i> (L.)	N. Italy	L	Batra, pest of cereals
<i>Phyllotreta</i> sp.	N. Yugoslavia	L	Batra
<i>Phyllotreta vittata</i> (F.)	N. Yugoslavia	L	Batra
<i>Phyllotreta vittula</i> Redtenbacher	E. Austria, N. Yugoslavia	R	Batra, pest of cereals
<i>Psylliodes picina</i> (Marsh)	Europe	L, S	Balachowsky, 1963
* <i>Pyrhalta calvariensis</i> (L.)	N. Italy, E. Austria	L, F	Batra, reared; Boldt; Mendl; Freude et al., 1966; Hering, 1957, Zocchi, 1953, abundant
* <i>Pyrhalta pusilla</i> (Duftschmidt)	N. Italy, E. Austria, N. Yugoslavia	L, mines	Batra; Freude et al., 1966; Hering, 1957, Boldt
Curculionidae			
<i>Anthonomus rubi</i> (Herbst)	N. Austria, S. Sweden, N. Italy	L, F	Batra; Boldt, pest of Rosaceae
<i>Apion sanguineum</i> (DeGeer)	N. Yugoslavia	L	Batra; <i>Lythrum</i> prob. not host
<i>Apoderus erythropterus</i> Zschach	Europe	L	Hoffmann, 1954; polyphagous
* <i>Hylobius transversovittatus</i> (Goeze)	Italy, E. Austria	R, St	Boldt; Mendl; Hoffmann, 1954; Scherf, 1964

Table 1. Continued.

Taxon	Location	Plant Part	Recorder/Remarks
<i>Lixus iridus</i> Olivier	Italy	St	Boldt, polyphagous
* <i>Nanophyes annulatus</i> Arag.	W. Europe, N. Yugoslavia	L galls	Batra, reared; Hoffmann, 1958; Dieckmann, 1963
* <i>Nanophyes brevis</i> Boheman	E. Austria, S. Europe	S, F	Mendl; Hoffmann, 1958
* <i>Nanophyes circumscriptus</i> Aubé	N. & C. Europe	St, L galls	Hoffmann, 1958; Dieckmann, 1963; Buhr, 1964
* <i>Nanophyes globiformis</i> (Kiesenwetter)	S. & C. Europe	St galls	Dieckmann, 1963
* <i>Nanophyes helveticus</i> Tournier	S. & C. Europe	St galls	Dieckmann, 1963
<i>N. hemisphaericus</i> Olivier	C. Europe	St	Hoffmann, 1958; Buhr, 1964
<i>Nanophyes marmoratus</i> (Goeze)	N. Yugoslavia, S. Sweden, Italy, E. Austria, Europe	F, S	Batra, reared; Boldt; Mendl; Hoffmann, 1958; Scherf, 1964; very common
<i>Nanophyes nitidulus</i> Gyllenhal	S. & C. Europe, N. Africa	St galls	Hoffmann, 1958; Dieckmann, 1963; usually on <i>L. hyssopifolia</i>
<i>Nanophyes yvonnae</i> Hoffmann	W. Europe	?	Hoffmann, 1958
<i>Phytobius comari</i> (Herbst)	Europe	L	polyphagous, Hoffmann, 1954; Scherf, 1964
Elateridae			
<i>Adrastus rachifer</i> (Fourcroy)	E. Austria	L	Batra; biology unknown
<i>Silesis</i> sp.	N. Yugoslavia	L	Batra
Helodidae			
<i>Cyphon</i> sp.	E. Austria	L	Batra
Melyridae			
<i>Malachius</i> , prob. <i>bipustulatus</i> (L.)	N. Yugoslavia	L	Batra
Collembola			
Entomobryidae			
<i>Deuterosminthurus repandus</i> Agren	E. Austria	L	Batra
<i>Entomobrya nivalis</i> L.	E. Austria, S. Sweden	L, St	Batra
<i>Lepidoceptus pusillus</i> L.	E. Austria	L, St	Batra
<i>Tomocerus</i> sp.	S. Sweden	L, St	Batra
Diptera			
Cecidomyiidae			
* <i>Dasineura salicariae</i> (Kieffer)	E. Austria, N. Yugoslavia, N. Europe, S. Italy	St bud galls	Batra, reared; Boldt, Buhr, 1964
Hemiptera			
Berytidae			
<i>Metacanthus meridionalis</i> (Costa)	Europe	L ?	Wheeler and Schaefer, 1982

Table 1. Continued.

Taxon	Location	Plant Part	Recorder/Remarks
Coreidae			
<i>Syromastes marginatus</i> (L.)	E. Austria	L	Batra
Lygaeidae			
<i>Cymus melanocephalus</i> (Fieber)	N. Yugoslavia	L	Batra
<i>Cymus</i> sp.	E. Austria	L	Batra
<i>Nysius</i> nr. <i>ericae</i> Schilling	Italy	L, F	Boldt
Miridae			
<i>Adelphocoris lineolatus</i> (Goeze)	N. Yugoslavia, Italy	L, F	Batra; Boldt; polyphagous, also in U.S.
<i>Adelphocoris seticornis</i> (F.)	N. Yugoslavia	L	Batra, usual hosts Leguminosae
<i>Campylomma verbasci</i> (Meyer-Dür)	E. Austria	L	Batra, polyphagous
<i>Calocoris roseomaculatus</i> (DeGeer)	N. Yugoslavia	L	Batra, usual hosts Asteraceae
<i>Liocoris tripustulatus</i> (F.)	N. Yugoslavia	L	Batra, usual hosts nettles
<i>Lygus</i> sp.	Italy, E. Austria	L, F	Boldt; Mendl
<i>Lygus pratensis</i> (L.)	N. Yugoslavia	L	Batra, polyphagous
<i>Lygus rugulipennis</i> Poppius	N. Yugoslavia, E. Austria	L	Batra, polyphagous
Mirinae spp. nymphs	N. Yugoslavia	L, F	Batra
Orthotylinae sp.	N. Yugoslavia	L	Batra
<i>Plagiognathus alpinus</i> Reuter	N. Yugoslavia	L	Batra
<i>Plagiognathus arbustorum</i> (F.)	S. Sweden, E. Austria, N. Yugoslavia	L	Batra, polyphagous
<i>Plagiognathus chrysanthemi</i> (Wolff)	E. Austria, S. Sweden	L, F	Batra, usual hosts Asteraceae
<i>Stenodema calcaratum</i> (Fallén)	E. Austria	L	Batra, usual hosts grasses
<i>Stenodema laevigatum</i> (L.)	N. Yugoslavia	L	Batra, usual hosts grasses
Pentatomidae			
<i>Carpocoris pudicus</i> (Poda)	N. Yugoslavia	L	Batra
<i>Dolycoris baccarum</i> (L.)	E. Austria	L	Batra, polyphagous
<i>Eysarcoris</i> nr. <i>inconspicuus</i> (Herrich-Schäffer)	Sardinia	L	Boldt
<i>Holcostethus</i> sp.	Italy	L	Boldt
Homoptera			
Aphididae			
<i>Aphis fabae</i> Scopoli	E. Austria, Europe	L	Mendl; Buhr, 1964
<i>Aphis gossypii</i> Glover	S. Italy	L	Boldt
<i>Aphis salicariae</i> Koch	Europe	L	Patch, 1938
<i>Myzus lythri</i> (Schrank)	Italy, Sardinia, N. Yugoslavia, E. Austria	L	Batra; Boldt, abundant
Cercopidae			
<i>Aphrophora alni</i> (Fallén)	E. Austria	L	Batra
<i>Cercopis sanguinolenta</i> (Scopoli)	S. Italy	L, F, S	Boldt

Table 1. Continued.

Taxon	Location	Plant Part	Recorder/Remarks
<i>Lepyronia coleoptrata</i> (L.)	N. Yugoslavia	L, S	Batra
<i>Philaenus spumarius</i> (L.)	S. Italy, N. Yugoslavia, E. Austria	L, F, S	Batra; Boldt, polyphagous pest
Cicadellidae			
<i>Cicadella viridis</i> (L.)	Italy, N. Yugoslavia	L	Batra; Boldt
<i>Empoasca</i> (<i>Kybos</i>) <i>butleri</i> Edwards	N. Yugoslavia	L	Batra
<i>Empoasca decipiens</i> Paoli	N. Yugoslavia	L	Batra
<i>Empoasca</i> sp.	S. Italy	L	Boldt
<i>Mocuellus metrius</i> (Flor)	E. Austria	L	Batra
<i>Typhlocyba</i> sp.	S. Sweden	L	Batra
Coccidae			
<i>Ceroplastes sinensis</i> Del Guercio	Italy	L	Boldt
Delphacidae			
Delphacid nymph	E. Austria	L	Batra
Membracidae			
<i>Stictocephala bisonia</i> Kopp & Yonke	E. Austria	L	Batra, pest
Pseudococcidae			
<i>Pseudococcus affinis</i> (Maskell)	S. Italy	L	Boldt
Tettigometridae			
<i>Tettigometra</i> sp.	Sardinia	L	Boldt
Hymenoptera			
Tenthredinidae			
<i>Ametastegia glabrata</i> (Fallén)	E. Austria	L	Batra; Mendl; polyphagous, also in N. America
Lepidoptera			
Arctiidae sp.	Yugoslavia	L	Batra
Coleophoridae			
<i>Coleophora paripennella</i> Zeller	Europe	L	Hering, 1957, polyphagous
Gelechiidae			
<i>Monochroa</i> (<i>Xystophora</i>) <i>conspersella</i> (Herrich-Schäffer)	Europe	L	Hering, 1957
Geometridae			
Geometrid spp.	N. Yugoslavia	L	Batra
<i>Chloroclystis v-ata</i> Haworth	E. Austria, Europe	L	Mendl; Hering, 1957; Elmquist, 1978; polyphagous
<i>Ematurga atomaria</i> (L.)	N. Yugoslavia	L	Batra, reared
<i>Eupithica</i> spp.	Italy, S. Sweden	L, F	Batra; Boldt, abundant
Gracillariidae			
<i>Calybitis phasianipennella</i> (Hübner)	Europe	L	Hering, 1957
Noctuidae			
Noctuid spp.	N. Yugoslavia, E. Austria	L	Batra

Table 1. Continued.

Taxon	Location	Plant Part	Recorder/Remarks
<i>Caloptusia</i> sp.	S. Sweden	St	Batra
<i>Polia oleracea</i> L.	E. Austria	L	Mendl
Psychidae			
<i>Apterona paludella</i> Dun- nehl	Europe	L	Hering, 1957
Sphingidae			
<i>Deilephila elpenor</i> L.	E. Austria	L	Mendl, polyphagous
<i>Deilephila</i> prob. <i>porcellus</i> L.	E. Austria	L	Batra, reared
Tortricidae			
Tortricid spp.	E. Austria, N. Italy, N. Yugoslavia	L	Batra
Olethreutinae sp.	N. Yugoslavia	L	Batra, reared
<i>Acleris</i> sp.	E. Austria	L	Batra
* <i>Acleris lorquiniana</i> Du- ponchel	N. Europe	F	Hannemann, 1961
<i>Syndemis musculana</i> (Hübner)	N. Europe	L	Hannemann, 1961
Lycaenidae			
Lycaenid sp.	N. Italy, N. Yugo- slavia	L	Batra
<i>Syntarucus pirithous</i> (L.)	S. Italy	F	Boldt, abundant
Orthoptera			
Acrididae			
<i>Odontopodisma schmidtii</i> (Fieber)	N. Yugoslavia	L	Batra
Tettigoniidae			
<i>Conocephalus</i> sp.	N. Yugoslavia	L	Batra
<i>Phaneroptera nana nana</i> Fieber	N. Yugoslavia	L	Batra
Psocoptera			
Amphilpsocidae			
<i>Graphopsocus cruciatus</i> L.	N. Yugoslavia	L	Batra
Lachesillidae			
<i>Lachesilla pedicularia</i> (L.)	E. Austria	L	Batra
Thysanoptera			
Thysanoptera spp.	Europe	L, F, St	Batra; Boldt
Thripidae			
<i>Taeniothrips discolor</i> (Karny)	Europe	F	Priesner, 1928, polypha- gous
<i>Thrips</i> sp.	E. Austria	F	Mendl
<i>Thrips discolor</i> (Karny)	Europe	F	Priesner, 1928, polypha- gous

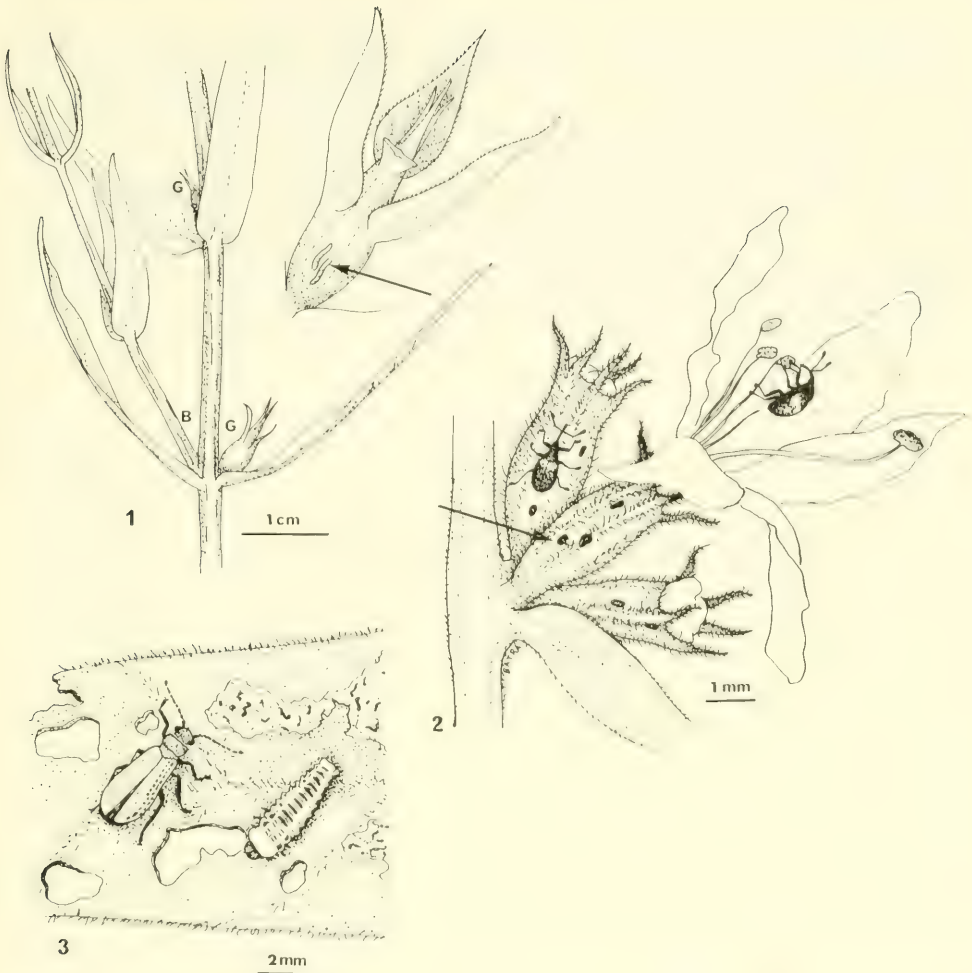
The cecidomyiid, *Dasineura salicariae* (Fig. 1), is widespread in the cool climates of northern and central Europe and is specific to *L. salicaria* (Buhr, 1964). It forms galls in the apical and axillary meristems, which effectively prevent flowering and branching. In some locations we found that all axillary buds of some plants were galled and aborted. These galls can reduce foliage production by 75%, and reduce growth of flowering spikes and thus seed production by 80%.

Table 2. Floral visitors of *Lythrum salicaria*.

Taxon	Location	Recorder/Remarks
Coleoptera		
Mordellidae		
<i>Mordella</i> sp.	N. Italy	Boldt
Nitidulidae		
<i>Brachypterolus pulicarius</i> (L.)	N. Yugoslavia	Batra
<i>Epuraea</i> sp.	E. Austria	Batra, larvae damage flowers
<i>Meligethes</i> 2 spp.	E. Austria, N. Yugoslavia	Batra, larvae damage flowers
Oedemeridae		
<i>Oedemera subulata</i> (Olivier)	N. Yugoslavia	Batra
Orthoperidae		
<i>Sericoderus</i> sp.	N. Italy	Batra
Phalacridae		
<i>Olibrus</i> sp.	N. Yugoslavia	Batra; Asteraceae usual hosts
Diptera		
Anthomyiidae		
<i>Delia platura</i> Meigen	E. Austria	Batra
Calliphoridae		
<i>Pollenia</i> sp.	E. Austria	Batra
Ceratopogonidae		
<i>Forcipomyia</i> (<i>Thyridomyia</i>) sp.	E. Austria	Batra
Chironomidae		
Chironomid sp.	E. Austria	Batra
Chloropidae		
<i>Meromyza</i> sp.	E. Austria	Batra
<i>Tricimba cincta</i> (Meigen)	N. Italy, N. Yugoslavia, E. Austria	Batra
Dolichopodidae		
<i>Chrysotus</i> sp.	N. Yugoslavia	Batra
Empididae		
Empidid sp.	E. Austria	Batra
Muscidae		
<i>Coenosia</i> nr. <i>antennata</i> Wiedemann	N. Yugoslavia	Batra
Scatopsidae		
<i>Scatopse</i> sp.	E. Austria	Batra
Sciaridae		
<i>Bradysia</i> spp.	E. Austria	Batra
<i>Sciara</i> sp.	E. Austria	Batra
Simuliidae		
<i>Simulium</i> sp.	E. Austria	Batra
Syrphidae		
<i>Episyrphus balteatus</i> (DeGeer)	E. Austria, Sardinia	Batra; Boldt
<i>Eristalis tenax</i> (L.)	E. Austria	Batra
<i>Helophilus pendulus</i> (L.)	E. Austria	Batra
<i>Neoascia podagrica</i> (F.)	N. Yugoslavia	Batra
<i>Platycheirus pelatutus</i> (Meigen)	E. Austria	Batra
<i>Platycheirus</i> sp.	N. Yugoslavia	Batra
<i>Scaeva pyrastris</i> (L.)	E. Austria	Batra
<i>Sphaerophoria</i> spp.	E. Austria, N. Yugoslavia	Batra
<i>Syritta pipiens</i> (L.)	N. Yugoslavia	Batra
Syrphid sp.	E. Austria	Batra

Table 2. Continued.

Taxon	Location	Recorder/Remarks
Hemiptera		
Anthocoridae		
<i>Anthocoris nemorum</i> (L.)	E. Austria	Batra
<i>Anthocoris pilosus</i> (Jakovelev)	N. Yugoslavia	Batra
<i>Orius majusculus</i> (Reuter)	E. Austria, N. Yugoslavia	Batra
<i>Orius minutus</i> (L.)	E. Austria, N. Yugoslavia, Italy, Sicily	Batra, reared; Boldt, abundant
<i>Orius niger</i> (Wolff)	Italy, N. Yugoslavia, E. Austria	Batra, reared; Boldt
Hymenoptera		
Apidae		
<i>Apis mellifera</i> L.	N. Yugoslavia	Batra
<i>Bombus lapidarius</i> (L.)	N. Yugoslavia	Batra
<i>Bombus lucorum</i> (L.)	Poland, N. Yugoslavia	Batra; Banaszak, 1973
<i>Bombus pascuorum</i> (Scopoli)	Poland	Banaszak, 1973
<i>Psithyrus</i> sp.	N. Yugoslavia	Batra
Anthophoridae		
<i>Ceratina callosa</i> (F.)	USSR	Pesenko, 1974
<i>Ceratina cyanea</i> (Kirby)	Poland	Banaszak, 1973
<i>Nomada emarginata</i> Morawitz	USSR	Pesenko, 1974
<i>Tetralonia nana</i> Morawitz	USSR, N. Yugoslavia	Batra, Pesenko, 1974
<i>Tetralonia salicariae</i> (Lepeletier)	USSR, Hungary	Pesenko, 1974; Tanacs, 1978
<i>Triepeolus tristis</i> Smith	USSR	Pesenko, 1974
Bethylidae		
<i>Goniozus</i> sp.	N. Italy	Batra
Chalcididae		
<i>Chalcis</i> sp.	E. Austria	Batra
Eulophidae		
<i>Tetrastichus</i> sp.	E. Austria, N. Italy	Batra
Formicidae		
<i>Dolichoderus quadripunctatus</i> (L.)	N. Italy	Batra
<i>Myrmica rubra</i> (L.)	E. Austria	Batra
<i>Plagiolepis pygmaea</i> (Latreille)	N. Italy	Batra
Halictidae		
<i>Evylaeus</i> sp.	N. Yugoslavia	Batra
<i>Ichneumonoides</i> spp.	E. Austria	Batra
Megachilidae		
<i>Anthidium florentinum</i> F.	N. Yugoslavia	Batra
<i>Megachile</i> sp.	N. Yugoslavia	Batra
<i>Megachile circumcincta</i> (K.)	Poland	Banaszak, 1973
Melittidae		
<i>Melitta haemorrhoidalis</i> (F.)	N. Yugoslavia	Batra, abundant
<i>Melitta nigricans</i> Alfken	Poland, Hungary	Banaszak, 1973; Tanacs, 1978
<i>Proctotrupoidea</i> sp.	E. Austria	Batra
Scelionidae		
<i>Telenomus</i> sp.	N. Italy	Batra
Tenthredinidae		
<i>Athalia rosae</i> (L.)	E. Austria	Batra, adult; larvae on Cruciferae
<i>Macrophya crassula</i> (Klug)	N. Yugoslavia	Batra, adult on <i>Sambucus</i>
Lepidoptera		
<i>Zygaenid</i> sp.	N. Yugoslavia	Batra



Figs. 1-3. Natural enemies of purple loosestrife in Europe. 1, Axillary galls (G) of *Dasineura salicariae*, which have prevented side branching (B) and growth of photosynthetic tissue and flower spikes. 1, Axillary gall of *D. salicariae* showing larvae in central chamber (arrow). 2, *Nanophyes marmoratus* on flowers, with characteristic holes (arrow), indicating damaged ovules. 3, *Pyrralta californiensis* adult and larva on foliage, with characteristic feeding marks.

Most *D. salicariae* galls were occupied by parasitic wasps, which must not be introduced into North America.

Other insects that are host-specific, according to the literature (Table 1), and may be useful for biological control, are the uncommon univoltine stem and root-boring weevil *Hylobius transversovittatus*, the defoliating chrysomelids *Aphthona lutescens* and *Altica lythri*, and the multivoltine flower-destroying tortricid, *Acleris lorquiniana*.

We recommend that detailed ecological and host-specificity studies be initiated for *D. salicariae*, *H. transversovittatus*, *P. californiensis* and *P. pusilla*, which attack the photosynthetic tissue and supporting structures of existing plants, and for *N. marmoratus* and *N. brevis*, which destroy the profuse seeds.

In North America (Levin and Kerster, 1973; Teale, 1982), as well as in Europe

(Table 2) the open flowers of purple loosestrife are a rich nectar and pollen resource for a wide variety of beneficial insects including pollinating bees, adult parasitic wasps, and syrphid flies, as well as adults of phytophagous and saprophagous insects. For example, in the U.S. (Franklin Co., N.Y.), SWTB found that the flowers are visited by numerous male and worker bumble bees (*Bombus bimaculatus* Cresson, *B. pennsylvanicus* (DeGeer), *B. ternarius* Say, *B. vagans* Smith, and *B. perplexus* (Cresson)), other bees (*Megachile melanophaca* Smith, *M. mendica* Cresson, *Anthophora furcata* Cresson, *Erylaeus leucozonius* (Schrank), *Dialictus versatus* (Robertson), *D. admirandus* (Sandhouse) and *Halictus confusus* (Smith)), butterflies (*Polites* sp.) and syrphid flies. The effects of large stands of flowering purple loosestrife on insect populations and insectivores in our wetlands are unknown, but may be significant.

ACKNOWLEDGMENTS

We thank the following specialists for identifying most of the insects associated with purple loosestrife: R. W. Carlson, D. C. Ferguson, R. J. Gagné, R. D. Gordon, E. E. Grissell, T. J. Henry, J. M. Kingsolver, J. P. Kramer, P. M. Marsh, A. S. Menke, D. A. Nickle, C. W. Sabrosky, T. J. Spilman, D. R. Smith, F. C. Thompson, D. M. Wiesman, R. E. White, D. R. Whitehead, and W. W. Wirth of the Systematic Entomology Laboratory, BBH, Agricultural Research Service, USDA and cooperating scientists W. A. Connell, E. L. Mockford, W. E. Steiner, Jr., and D. L. Wray; also M. Daccardi, F. Kasy, and L. Dieckmann. E. M. Barrows, J. J. Drea, and R. J. Gagné reviewed the manuscript. We particularly thank D. Q. Thompson, formerly of USDI Fish and Wildlife Service, for his encouragement to undertake this research and for providing some references.

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RHYACOPHILA KONDRATIEFFI
(TRICHOPTERA: RHYACOPHILIDAE), A NEW
SPECIES FROM VIRGINIA

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Abstract.—*Rhyacophila kondratieffi*, n. sp., is described from southwestern Virginia. The species lives in first and second order mountain streams.

An undescribed species of *Rhyacophila* was discovered among specimens of Trichoptera collected by Boris C. Kondratieff from Little Rock Castle Creek, a second order spring-fed stream in Patrick County, Virginia. Further collecting by Dr. Kondratieff in similar habitats in Grayson and Smyth counties resulted in additional specimens.

The new species is a member of the *invaria* subgroup of the *Rhyacophila invaria* group of species (Schmid, 1970). It is most closely related to *R. banksi* Ross, *R. parantra* Ross, and *R. shenandoahensis* Flint as evidenced in the males by the concave segment X, the elongate anal sclerites with small apical lobes and horizontally produced lateral winglets ("petites aillettes laterales horizontales," Schmid, 1970:61), the bilobed apical segment of the inferior appendages having the dorsal lobe approximately half the length of the ventral lobe, and the large phallic apparatus having spiniform parameres and prominent membranous ventral lobes. With the females of the *invaria* subgroup, the new species shares the ventral median process and dorsal notch of the posterior margin of segment VIII and simple vaginal sclerites with an elongate, curved terminal sclerite and reduced lateral sclerites.

***Rhyacophila kondratieffi* Parker, NEW SPECIES**

Adult.—Structure typical for genus. Color of specimens in alcohol brown. Forewing 7-9 mm in length. Sternum of abdominal segment VII with small median apical projection. *Male genitalia* (Fig. 1a-d): Segment IX (Fig. 1a) narrow ventrally with prominent longitudinal strengthening ridge at articulation with inferior appendage, abruptly widened above strengthening ridge; dorsal apical lobe (Fig. 1a) extending over body of segment X and anal sclerites, obscuring them in dorsal aspect (Fig. 1b), apical margin irregular, apex rounded to triangular. Body of segment X (Fig. 1a) large, concave, occupying concavity in segment IX between inferior appendage and dorsal apical lobe of segment IX, bearing prominent setae around outer margin and stouter setae on raised protuberances on posterior concave surface (Fig. 1c); anal sclerite sinuous in lateral aspect (Fig. 1a) with long basal portion extending into segment IX and having enlarged apical portion pro-

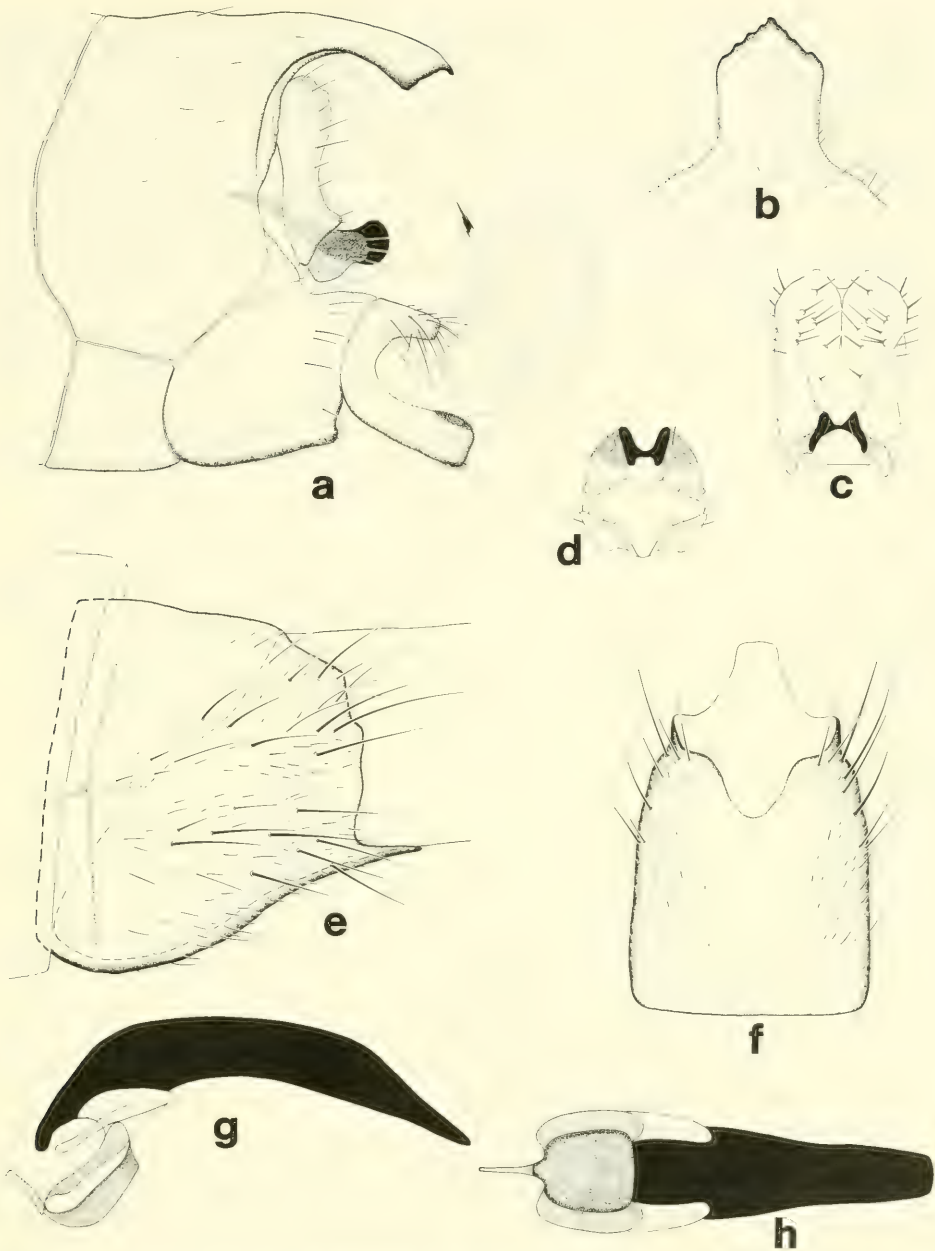


Fig. 1. *Rhyacophila kondratieffi* genitalia. a, Male, lateral. b, Male, dorsal apical lobe of segment IX, dorsal. c, Male, body of segment X and anal sclerites, caudal. d, Male, body of segment X and anal sclerites, dorsal. e, Female, segment VIII, lateral. f, Female, segment VIII, dorsal. g, Female, vaginal sclerites, lateral. h, Female, vaginal sclerites, ventral.

duced posteriorly into darkly sclerotized rounded lobe bearing numerous minute spicules, produced laterally into lightly sclerotized triangular projection; anal sclerite in dorsal aspect (Fig. 1d) with posterior apical lobes separated medially by broad U-shaped cleft. Inferior appendage (Fig. 1a) having basal segment quadrate, apical segment bilobed with dorsal lobe approximately one-half length of ventral lobe and bearing several long posteroventrally directed setae, ventral lobe bearing conspicuous patch of peg-like setae. Phallic apparatus (Fig. 1a) large, paramere membranous with spiniform apex, aedeagus lightly sclerotized. *Female genitalia* (Fig. 1e-h): Segment VIII with ventral median projection (Fig. 1f) truncate or emarginate apically, lateral margin (Fig. 1e) without prominent projections or emarginations, dorsal margin (Fig. 1f) with broad smooth U-shaped notch. Vaginal sclerites brown, terminal sclerite elongate, decurved in lateral aspect (Fig. 1g) and uniform in width throughout most of length with posterior third tapered to acute apex, in ventral aspect (Fig. 1h) broadest anteriorly and ending in truncate or slightly emarginate apex, lateral margins sinuous; lateral sclerites small and widely separated ventrally (Fig. 1h), connected to basal ring by cup-shaped median sclerite.

Types.—Holotype, ♂, VIRGINIA: Patrick County, Little Rock Castle Creek, Rt. 605 off Rt. 8, 13 May 1979, B.C. Kondratieff. Paratypes, VIRGINIA: same data as holotype, 32 ♂ and 10 ♀; same data, P. Firth (PF79-17-2), 2 ♂ and 4 ♀. Grayson County, Lewis Fork, Rt. 603, 30 May 1981, B.C. Kondratieff, 4 ♂. Smyth County, headwater springs of Grindstone Branch, Grindstone Cpgd., Rt. 603, 30 May 1981, B.C. Kondratieff, 3 ♂; Grindstone Branch, Grindstone Cpgd., 7 July 1980, B.C. Kondratieff, 2 ♂.

All specimens are deposited in the collection of the National Museum of Natural History.

Etymology.—This species is named in honor of Boris C. Kondratieff, a friend of the author, an outstanding entomologist, and an avid collector who has contributed much to the study of aquatic insects.

Diagnosis.—Males of *Rhyacophila kondratieffi* are easily distinguished from males of the other species in the *invaria* subgroup by the long undivided dorsal apical lobe of segment IX which extends posteriorly beyond the apex of segment X and the anal sclerites. The females are distinguished by having the ventral projection of segment VIII truncate or only slightly emarginate, and having the lateral margin simple rather than sinuous, incised, or bearing a sharp tooth, and by the shape of the vaginal apparatus.

Remarks.—There is considerable morphological variation within all of the species in this subgroup. Males of *kondratieffi* are no exception, particularly in the shape of the dorsal apical lobe of segment IX and the apical segment of the inferior appendages. Specimens from Smyth County tend to have a less angular, more rounded outline to the dorsal apical lobe than specimens from Patrick County. Specimens from Grayson County are similar to those from Smyth County, except that the dorsal apical lobe is more irregular. Specimens from both Smyth and Grayson counties, as well as some specimens from Patrick County have the apex of the dorsal lobe of the apical segment of the inferior appendage acute or rounded. Specimens from these localities also have the apex of the ventral lobe rounded rather than truncate as in the holotype (Fig. 1a) and many other specimens from Patrick County.

The phylogenetic relationships of *kondratieffi*, *banksi*, *parantra*, and *shenandoahensis* are difficult to determine. The fact that all four species occur in isolated populations in small spring-fed streams has resulted in their being infrequently encountered by most collectors and thus not well represented in collections. Schmid (1970) treats *banksi*, *parantra*, and *shenandoahensis* as an unresolved trichotomy. According to Schmid, a prominent undivided dorsal apical lobe of segment IX represents the ancestral condition within *Rhyacophila*. On the other hand, Ross (1956) apparently considers the absence of a dorsal apical lobe to represent the ancestral condition in *Rhyacophila*. There is insufficient information available about other characters to resolve the question of the relationships of the species of the *invaria* subgroup.

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***Aedes (Stegomyia) corneti*, A NEW SPECIES OF THE
Africanus SUBGROUP (DIPTERA: CULICIDAE)¹**

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Abstract.—Adults of both sexes and the larva and pupa of *Aedes (Stegomyia) corneti* n. sp. from Sierra Leone are described and illustrated. Diagnostic characters for separating the adults of *Ae. corneti* from closely allied species are given. The distribution of *Ae. corneti* is based on examined specimens.

A new species of *Aedes (Stegomyia)* belonging to the *africanus* subgroup of the *aegypti* group was recently collected while conducting field work in Sierra Leone in 1984. This new species, which is extremely similar in overall habitus to adults of *Aedes (Stegomyia) africanus* (Theobald), 1901, was found also among specimens misidentified as *Ae. africanus* from the Services Scientifiques Centraux, Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM), Institut Pasteur, Paris (PIP) and the British Museum (Natural History) collections.

In view of the medical importance of several species in the *africanus* subgroup and the similarity of this new species with *Ae. africanus* (Theobald), it is desirable to describe the new species here to make its name available and to avoid future confusion between it and *Ae. africanus*. Because nothing is known about its biting habits and its potential as vector of human pathogens, it is hoped that this paper will stimulate investigations on these subjects.

MATERIALS AND METHODS

This study is based on specimens collected by the Systematics of *Aedes* Mosquitoes Project (SAMP), Department of Entomology, National Museum of Natural History, Smithsonian Institution (USNM), and on specimens borrowed from institutions mentioned in the acknowledgments section. Distributional records are listed in the following order and format: country names are in capital letters, administrative divisions, where known, are in italics, and place names have the first letter capitalized.

The terminology follows that of Harbach and Knight (1980), with the exception of "tarsal claws," which is retained for "unguis." The venational terms follow those of Belkin (1962).

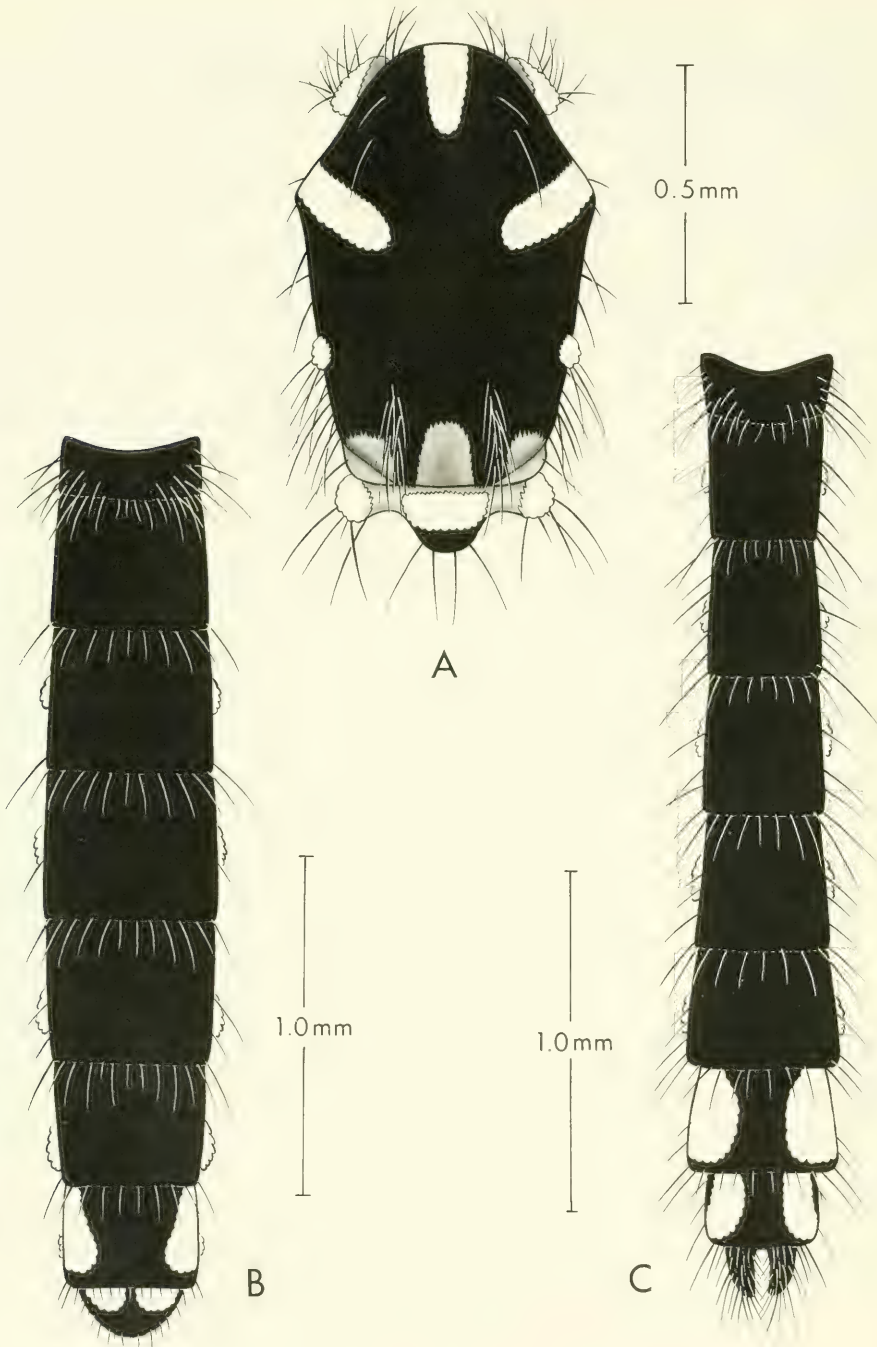
¹ This work was supported by Grant No. DAMD-17-84-G-4033 from the U.S. Army Medical Research and Development Command, Office of the Surgeon General, Fort Detrick, Frederick, MD 21701, and by the Walter Reed Biosystematic Unit, Museum Support Center, Smithsonian Institution, Washington, D.C. 20560.

Aedes (Stegomyia) corneti Huang, NEW SPECIES

Figs. 1–5

Female.—*Head*: Proboscis dark scaled, without pale scales on ventral surface, longer than forefemur (1.26–1.31 length of forefemur); maxillary palpus about 0.19 length of proboscis, dark, with white scales on entire dorsal surface of palpomere 4; pedicel covered with white scales except on dorsal surface; antenna with a few dark scales on flagellomere 1; clypeus bare; occiput with few erect forked scales; a row of broad white scales around eye margins; vertex with a median stripe or patch of broad white scales, with broad dark scales on each side interrupted by lateral stripe of broad white scales, followed ventrally by a patch of broad white scales. *Thorax* (Fig. 1A): Scutum with narrow dark scales, and a distinct median stripe of broad white scales on anterior promontory, a large patch of broad white scales on fossal area, a patch of broad white scales on lateral margin just in front of wing root; acrostichal setae absent; dorsocentral setae present; scutellum with broad white scales on all lobes and with a few broad dark scales at apex of midlobe; antepronotum with broad white scales; postpronotum with a patch of broad white scales; paratergite with broad white scales; postspiracular area without scales; hypostigmal area without scales; patches of broad white scales on propleuron, subspiracular area, upper and lower portions of mesokatepisternum, and on mesepimeron; upper mesokatepisternal scale patch not reaching to anterior corner of mesokatepisternum; upper mesepimeral scale patch connecting with lower mesepimeral scale patch; lower mesepimeron without setae; metameron and mesopostnotum bare. *Wing*: With dark scales on all veins except for a minute basal spot of white scales on costa; cell R_2 about 2.6 length of R_{2+3} . *Halter*: With dark scales. *Legs* (Fig. 2A): Coxae with patches of white scales; white knee-spot absent on femora; forefemur anteriorly with a narrow, white longitudinal stripe on ventral surface in apical 0.56; midfemur with 3 large, white patches on anterior surface (on basal, median and apical areas); hindfemur with 2 large, white patches on anterior surface (on median and apical areas); fore- and midtibiae anteriorly dark; hindtibia anteriorly dark, with a white longitudinal stripe on ventral surface in basal 0.20–0.25; fore- and midtarsi with a basal white band on tarsomeres 1, 2; hindtarsus with a basal white band on tarsomeres 1–4, the ratio of length of white band on dorsal surface to the total length of tarsomere is 0.22–0.25, 0.20–0.23, 0.82–0.88 and 0.33–0.50; tarsomere 5 all dark; fore-, mid- and hindlegs with tarsal claws equal, all toothed. *Abdomen* (Fig. 1B): Tergum I with white scales on laterotergite; terga II–VIII each with basolateral white spots which are not visible in dorsal aspect except on terga VII–VIII; sterna III–VII each with a basal white band; segment VIII largely retracted. *Genitalia*: Apical margin of sternum VIII with a median notch and with conspicuous rounded lateral lobes; insula longer than wide, with minute setae and with 3 larger setae on apical 0.25; apical margin of tergum IX with well developed lateral lobes, each with 2–6 setae; apical margin of postgenital plate with a median notch; cercus short and broad; 3 spermathecae, one larger than the other 2.

Male.—Essentially as in the female, differing in the following sexual characters: *Head*: Maxillary palpus slightly shorter than proboscis, predominantly dark, with a white band at base of palpomeres 2–5, those on palpomeres 4, 5 dorsally incomplete; palpomeres 4, 5 subequal, slender, dorsally curved and with only a few short setae; antenna plumose, shorter than proboscis. *Wing*: Cell R_2 about 2.1



Aedes (Stegomyia) corneti n. sp.

Fig. 1. *Aedes (Stegomyia) corneti* n. sp. A, Dorsal aspect of the allotype female thorax. B, Dorsal aspect of the allotype female abdomen. C, Dorsal aspect of the holotype male abdomen.

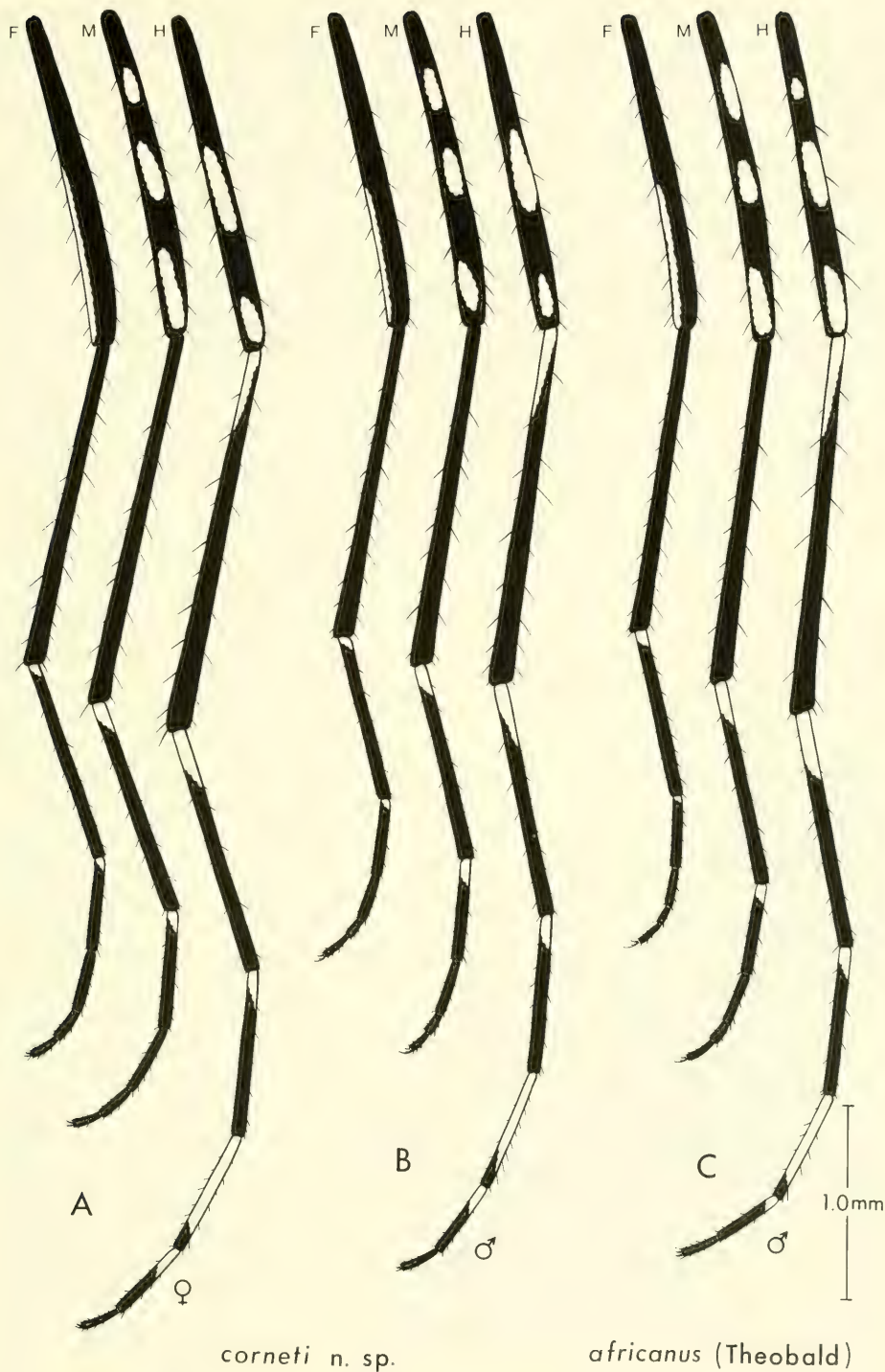
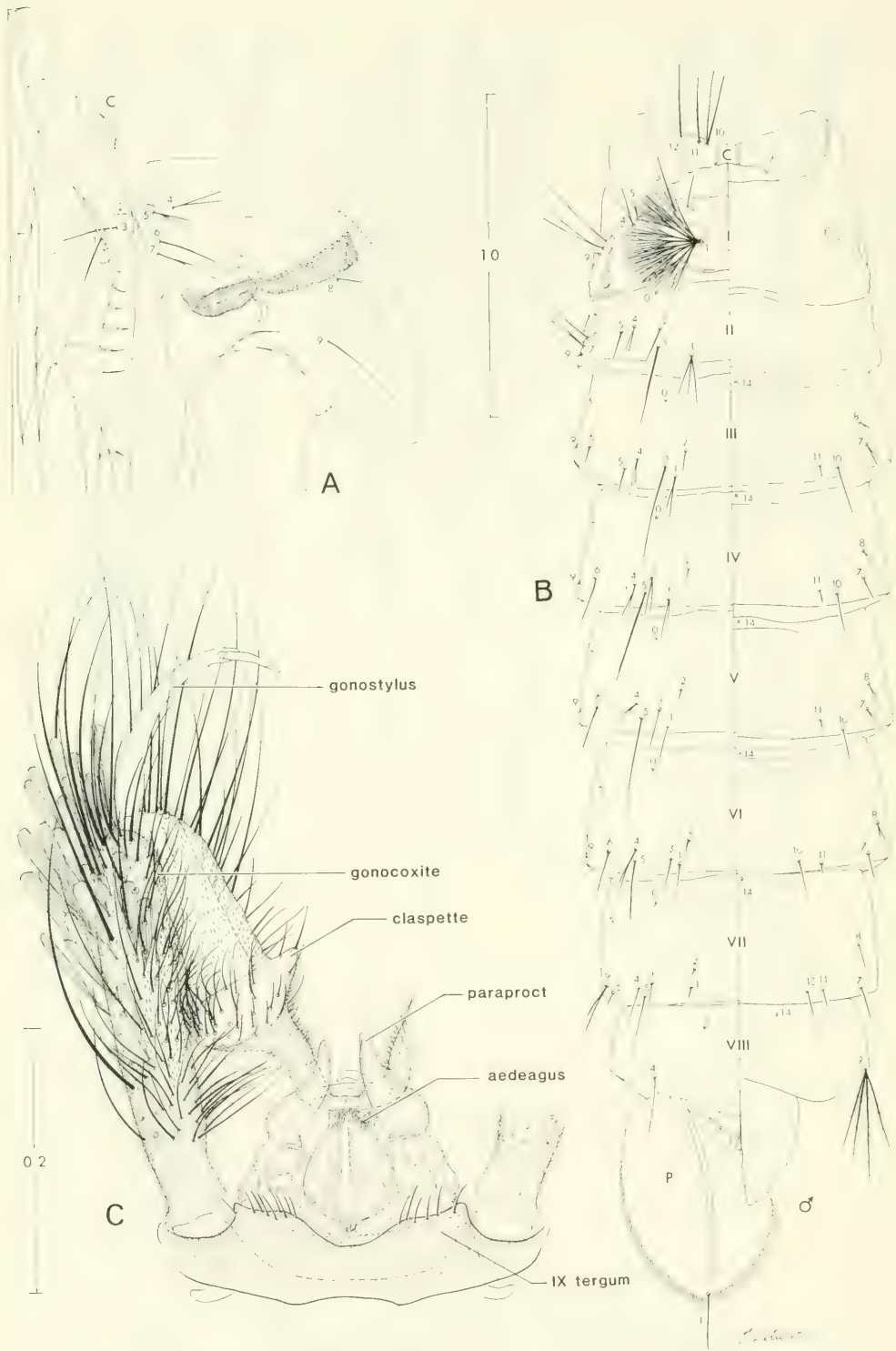


Fig. 2. A-B, *Aedes (Stegomyia) corneti* n. sp. A, Anterior surface of the female legs. B, Anterior surface of the male legs. C, *Aedes (Stegomyia) africanus* (Theobald), anterior surface of the male legs.



Aedes (Stegomyia) corneti n. sp.

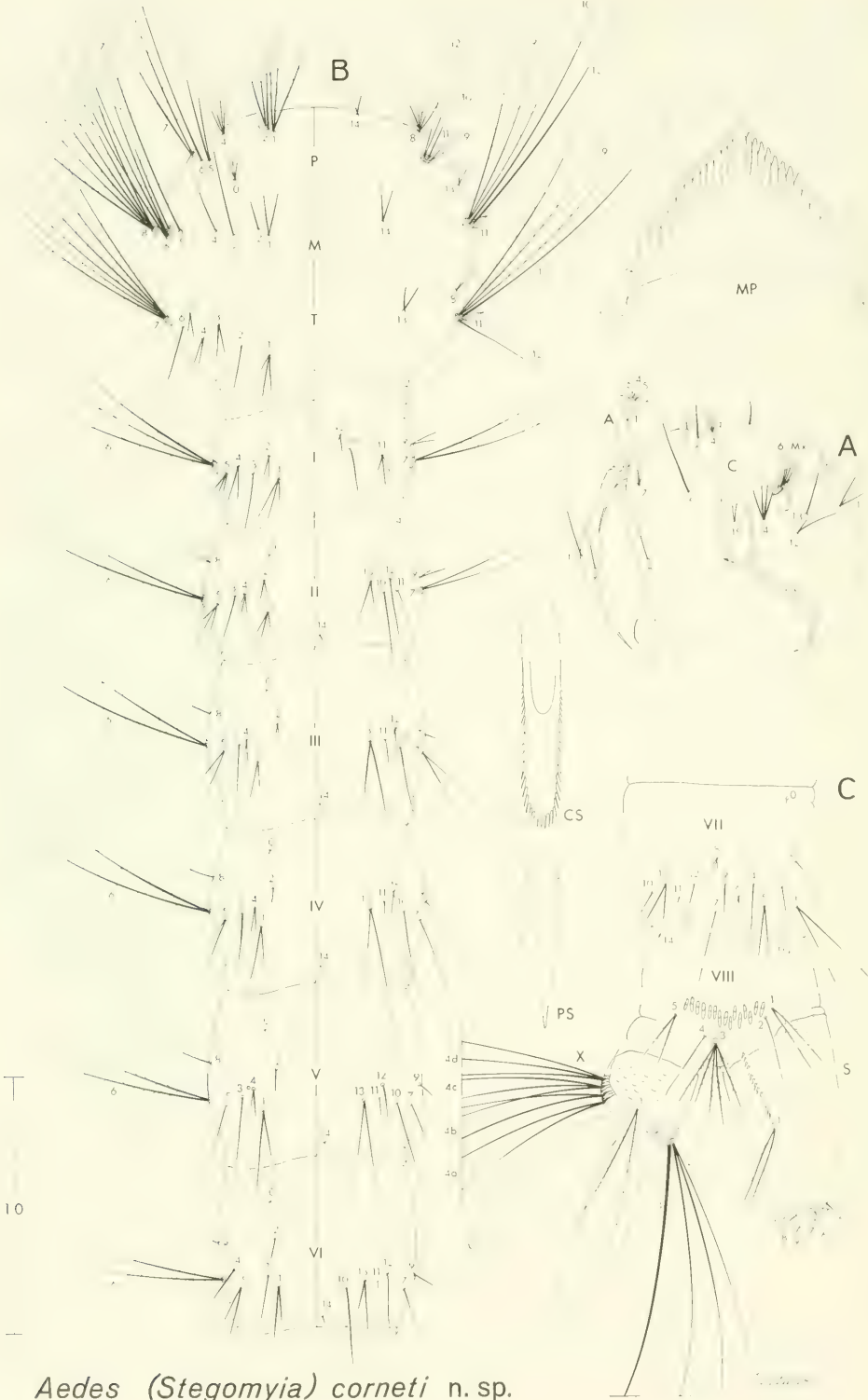
length of vein R_{2+3} . *Legs* (Fig. 2B): Hindtarsus with a basal white band on tarsomeres 1–4, the ratio of length of white band on dorsal surface to the total length of tarsomere is 0.25–0.30, 0.20–0.24, 0.81–0.87 and 0.30–0.44; fore- and midlegs with tarsal claws unequal, the smaller one toothed, the larger one simple. *Abdomen* (Fig. 1C): Sternum VIII with basolateral white spots. *Genitalia* (Fig. 3C): Gonocoxite 2.0–2.2 as long as wide (width measured 0.5 from base), scales restricted to dorsolateral, lateral and ventral surfaces, with setae on dorsomesal surface, mesal surface membranous; claspette large, lobed, subtriangular in shape in dorsal aspect, narrows towards apicomesal angle, broadened apicolaterally, with apicolateral corner rounded, and with numerous simple setae and with 1 somewhat stronger, spine-like seta on apicomesal angle of expanded distal lobe; gonostylus simple, elongate, about 0.6 length of gonocoxite, with a long slender claw process at apex and with a few setae in apical 0.25; aedeagus with short teeth only; paraproct with a sternal arm; cercal setae absent; apical margin of tergum IX concave medially with 3–12 setae on lateral lobe; sternum IX without setae.

Pupa (Figs. 3A, 3B).—*Cephalothorax*: Trumpet about 4.0 as long as wide (width measured 0.5 from base); setae 1, 3-CT single, longer than 2-CT; 2-CT single, small; 4-CT double; 5-CT usually with 3 branches (2–3); 6-CT single, stout, slightly longer than 7-CT; 7-CT usually double (1–2); 8-CT usually single (1–2); 9-CT single, longer than 8-CT; 10-CT usually double (1–3), caudomesad of 11-CT; 11-CT single, stout; 12-CT usually single (1–2). *Abdomen*: Seta 1-I well developed, with more than 10 dendritic branches; 2-I single; 3-I usually single (1–2), long; 2-I and 3-I widely separated, distance between their bases about 1.5 of distance between those of 4-I and 5-I; seta 1-II usually with 3 branches (2–8); 3-II, III usually single (1–2); 1-III usually double (1–3); 1-IV usually double (1–2); 2-IV, V anteromesad of 1-IV, V respectively; 5-IV–VI usually single (1–2), short, not reaching beyond posterior margin of following segment; seta 9-I–VI small, single, simple; 9-VII usually with 2 branches (1–2); 9-VII, VIII much longer and stouter than 9-I–VI; 9-VIII usually with 4 branches (2–4) and barbed. *Paddle*: Oval, about 1.4 as long as wide; margins with fringe of long hair-like spicules; seta 1-p single.

Larva (Fig. 4).—*Head*: Antenna short, less than 0.5 length of head, without spicules; seta 1-A inserted in apical 0.5 of shaft, single; inner mouthbrushes apically pectinate; seta 4-C well developed, usually with 5 branches (4–6), cephalomesad of 6-C; 5-C single, long; 6-C single; 7-C usually double (2–3); 8–10, 13-C single; 11-C usually with 3 branches (2–3), barbed; 12-C usually double (2–3); 14-C usually with 4 branches (3–7); 15-C usually double (2–3); mentum usually with 13 (12–14) teeth on each side of central tooth. *Thorax*: Seta 1-P usually with 3 branches (2–3), barbed; 2-P single; 3-P double; 4-P usually with 4 branches (3–6); 5-P usually double (2–3), barbed; 6-P single and barbed; 7-P double and barbed; 9-P usually double (1–2); 11-P single; 14-P usually double (2–3); 5, 7-M single and barbed; 6-M with 3 branches, barbed; 8-M usually with 6 branches (5–6), barbed; 9-M with 3 branches, barbed; 10, 12-M single, long, stout and barbed; 11-M single, small; 7-T usually with 6 branches (5–6), barbed; 9-T usually with

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Fig. 3. *Aedes (Stegomyia) corneti* n. sp. A, Dorsolateral aspect of the cephalothorax of the male pupa. B, Dorsal and ventral aspects of the metathorax and abdomen of the male pupa. C, Tergal aspect of the male genitalia.



Aedes (Stegomyia) corneti n. sp.

3 branches (2–3), barbed; 10, 11-T similar to those on mesothorax; 12-T much reduced, single and simple; basal spine of meso- and metapleural setae long, apically pointed. *Abdomen*: Seta 6-I usually with 3 branches (3–4), barbed; 7-I double, barbed; 6-II–VI double and barbed; 7-II double, barbed; 1-VII double; 2-VII single; 2-VIII distant from 1-VIII; 1-VIII usually double (2–3), barbed; 3-VIII usually with 5 branches (5–7), barbed; 5-VIII usually double (2–5), barbed; 2, 4-VIII single; comb of VIII with 10–15 scales in a row, each scale spatulate, with apex rounded and with fringe all round the apex; segment X with saddle incomplete, marginal spicules very small and inconspicuous; seta 1-X double and barbed; 2-X with 3 branches; 3-X single; 4-X with 4 pairs of setae on grid, 4a, b-X double, 4c, d-X with 2–3 branches; no precratal tufts; anal papillae subequal, about 2.8 length of saddle, sausage-like. *Siphon*: 2.0–2.5 as long as wide 0.5 from base, acus absent; usually with 15 (11–19) pecten spines, evenly spaced, each spine usually with a single well developed ventral denticle, sometimes with 1–2 small basal denticles also; seta 1-S double, inserted beyond apical pecten spine and in line with pecten spines.

Type data.—Holotype ♂ (SAMP Acc. 1093, SL 197-11) with associated larval and pupal skins on slides, with genitalia on slide (84/423), Tiwai Island (on the Moa River), Potoru, *Southern Province*, SIERRA LEONE, collected as larvae from a cut bamboo, about 0.33 m above ground level, partially shaded, in the forest, June 8, 1984, Y. M. Huang [USNM]. Allotype female (SAMP Acc. 1093, SL 197-17) with associated larval and pupal skins on slide, same data as holotype [USNM]. Paratypes: 5 ♂, 1 ♀ and 1 4th instar larva as follows (SAMP Acc. 1093): 5 ♂ (SL 197-14, 15, 16, 18, 20) with associated larval and pupal skins on slides, with genitalia on slides (84/424, 84/425, 84/426, 84/427, 84/428) and 1 ♀ (SL 197-21) with associated larval and pupal skins on slides, with genitalia on slide (86/138), same data as holotype [USNM]; 1 4th instar larva (SL 197), same data as holotype [USNM].

Other material examined.—CAMEROON (Cameroun). *East Cameroon*: Obala (4°10'N, 11°32'E), Aug. 14, 1964, A. Rickenbach (MEP Acc. 724), 1 ♂, 1 ♂ gen. (82/100) [ORSTOM]. *IVORY COAST*. *Sud Département*: Abidjan, Forêt du Banco (5°25'N, 4°03'W), P. Cachan, (MEP Acc. 723), 3 ♂, 2 ♀, 3 ♂ gen. (82/98, 82/99, 84/297) [PIP]; same data, (MEP Acc. 724), 15 ♂, 6 ♀, 15 ♂ gen. (82/120, 82/121, 82/122, 82/123, 82/125, 82/126, 82/127, 82/128, 82/141, 82/142, 84/301, 84/302, 84/303, 84/305, 84/309), 2 ♀ gen. (84/299, 84/300) [ORSTOM]; Cercle de Sassandra, Saoua (6°19'N, 5°10'W), Apr. 13, 1962, J. Hamon, (MEP Acc. 724), 2 ♂ (#620413C, #620413D), 2 ♂ gen. (84/321, 84/322) [ORSTOM]; same data except Apr. 24, 1962, 1 ♀ (#620413A) [ORSTOM]. *SIERRA LEONE*. *Southern Province*: Mabang (8°21'N, 11°51'W), 1926, R. M. Gordon, (MEP Acc. 719), 1 ♂ (#548), 1 ♂ gen. (82/83) [BM].

Distribution (Fig. 5).—*Aedes corneti* is presently known from Cameroon, the Ivory Coast and Sierra Leone. Other records of *Ae. africanus* from the Afrotropical Region will require confirmation owing to probable confusion with *Ae. corneti*.

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Fig. 4. *Aedes (Stegomyia) corneti* n. sp. A, Dorsal and ventral aspects of the head of the fourth instar larva. B, Dorsal and ventral aspects of the thorax and abdomen of the fourth instar larva. C, Lateral aspect of the terminal abdominal segments of the fourth instar larva.



Fig. 5. Distribution of *Aedes (Stegomyia) corneti* n. sp. in Africa.

Etymology.—This species is named to honor Dr. Michel Cornet, Medical Entomologist, Services Scientifiques Centraux de l'O.R.S.T.O.M. (ORSTOM), and Chief, Medical Entomology Laboratory, Institut Pasteur de Dakar, Senegal, in recognition and appreciation of his contributions to our knowledge of the mosquito fauna of Africa.

Taxonomic discussion.—*Aedes* (*Stegomyia*) *corneti* is a member of the *africanus* subgroup, which presently comprises at least seven species: *Ae. africanus* (Theobald), 1901; *Ae. luteocephalus* (Newstead, in Newstead et al., 1907); *Ae. pseudoafricanus* Chwatt, 1949; *Ae. ruwenzori* Haddow and Van Someren, 1950; *Ae. opok* Corbet and Van Someren, 1962; *Ae. neoafricanus* Cornet, Valade and Dieng, 1978 and *Ae. corneti* n. sp. These species form a unique subgroup within the *aegypti* group, and share the following combination of characters: (1) maxillary palpus possessing white scales; (2) scutum with dorsocentral setae present; (3) scutum with a distinct patch of broad white scales on fossal area; (4) subspiracular area with broad white scales; (5) postspiracular area without scales; (6) paratergite with broad white scales; (7) white knee-spot absent on femora; (8) hindtarsus with a basal white band at least on tarsomeres 1–3; and (9) hindtarsomere 5 all dark. However, *Ae. corneti* differs from all other members of the *africanus* subgroup by the following combination of characters: (1) scutum without a distinct median longitudinal yellow line of narrow scales; (2) posterior dorsocentral yellow or white line of narrow scales not developed; (3) terga II–VIII (II–VII in male) each with basolateral white spots only; (4) hindfemur with at most 2 large, white patches on anterior surface (on median and apical areas); (5) hindtibia with a white longitudinal stripe on ventral surface in basal 0.20–0.25; and (6) hindtarsomere 4 with basal 0.30 or more white.

The adult male and female of *Ae. corneti* are extremely similar to those of *Ae. africanus* with which it has been confused and misidentified. In addition, *Ae. corneti* has been found in association with *Ae. africanus* in a forest in the Ivory Coast. Thus, great care must be taken in identifying them. They can be distinguished easily from those of *Ae. africanus* by the hindfemur with at most 2 large, white patches on the anterior surface (on median and apical areas) and by the hindtarsomere 4 with the basal 0.30 or more white. In *Ae. africanus*, the hindfemur has 3 large, white patches on the anterior surface (on basal, median and apical areas), and the hindtarsomere 4 is 0.25 or less white basally (Fig. 2C).

The male genitalia of *Ae. corneti* are easily differentiated from all other species in the *africanus* subgroup by the claspette, which has the distal expanded portion subtriangular in shape in dorsal aspect (narrows towards the apicomesal angle, becomes broader apicolaterally, with apicolateral corner rounded), with numerous simple setae on the expanded distal portion and bearing 1 somewhat stronger, spine-like seta on the apicomesal angle.

Bionomics.—The larvae of *Ae. corneti* were collected from a cut bamboo, about 0.33 m above the ground level, partially shaded, in the forest, on Tiwai Island, and in tree holes, in Mabang, Sierra Leone. In the Ivory Coast, the immature stages of *Ae. corneti* were collected in bamboo pots that were placed in forest (Forêt du Banco), Abidjan, and in tree holes in Saoua, Cercle de Sassandra.

Aedes corneti has been collected in association with *Culex albiventris* Edwards and *Eretmapodites oedipodius* Graham from Tiwai Island, Sierra Leone. It has

also been found in association with *Ae. africanus* from forest (Forêt du Banco), Abidjan, Ivory Coast.

Medical importance.—Unknown. However, *Aedes africanus* has been recognized as one of the most important virus vectors of the Afrotropical Region (Haddow, 1961). In Uganda, *Ae. africanus* has been incriminated as the principal vector of yellow fever of the monkey to monkey cycle in Semliki Forest (Haddow, Smithburn et al., 1947; Haddow et al., 1948; Haddow and Mahaffy, 1949; Smithburn et al., 1949) and from monkey to man in Bwamba County (Haddow, 1945; Haddow et al., 1947; Lumsden, 1951; Haddow, 1968). In eastern Africa, at least four arboviruses have been isolated from *Ae. africanus*: yellow fever (Smithburn and Haddow, 1946; Smithburn et al., 1949; Haddow, 1968; Kirya et al., 1977), chikungunya (Weinbren et al., 1958; Haddow et al., 1961; McCrae et al., 1971), Rift Valley fever (Weinbren et al., 1957) and Zika (Dick et al., 1952; Weinbren and Williams, 1958; Haddow et al., 1964) in Uganda, and yellow fever in Ethiopia (Sérié et al., 1968).

Aedes africanus from Nigeria is an efficient vector of yellow fever under laboratory conditions, as shown by Philip (1929, 1930). It is recognized as a vector of yellow fever in West and Central Africa (Hamon et al., 1971, in West Africa; Rickenbach et al., 1971 and Germain et al., 1972, in Cameroon; Pajot, 1972 and Germain, Sureau et al., 1976, in Central African Republic; Bang et al., 1979, in Nigeria). In West and Central Africa, yellow fever virus has also been isolated from *Ae. africanus* in the Ivory Coast (Chippaux et al., 1975) and in the Central African Republic (Germain, Sureau et al., 1976); it has also been isolated from *Aedes (Stegomyia) opok* Corbet and Van Someren in the Central African Republic (Germain et al., 1976), *Aedes (Stegomyia) neoafricanus* Cornet, Valade and Dieng, and *Aedes (Stegomyia) luteocephalus* (Newstead) in Senegal (Cornet et al., 1978; Cornet et al., 1979). In addition to the yellow fever virus, chikungunya, Zika and Bouboui viruses have been isolated from *Ae. africanus* and *Ae. opok* in the Central African Republic (Germain et al., 1978), and chikungunya, Zika and dengue 2 viruses have been isolated from *Ae. luteocephalus* in Senegal (Cornet et al., 1979). Members of the *africanus* subgroup are involved in the enzootic-epizootic cycles of yellow fever in primates in West and Central Africa (Germain, Sureau et al., 1976; Cornet in WHO, 1978; Cornet et al., 1979).

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REVISION OF THE MICRO-CADDISFLY GENUS *OXYETHIRA*
(TRICHOPTERA: HYDROPTILIDAE)
PART III: SUBGENUS *HOLARCTOTRICHIA*

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Abstract.—The subgenus *Holarctotrichia* Kelley of the micro-caddisfly genus *Oxyethira* is revised. Two species groups are included. Species descriptions and illustrations as well as phylogenetic and biogeographical discussions of the eight known species are provided.

The micro-caddisfly genus *Oxyethira* Eaton is among the largest genera (in terms of numbers of species) in the family Hydroptilidae and is found in every biogeographical region. This study is the third part of a review of the genus (Kelley, 1984, 1985), and deals with the subgenus *Holarctotrichia* Kelley. Subgenus *Holarctotrichia* includes eight known species from the Holarctic Region. Within the subgenus are two distinct species groups, the nearctic forcipata group and the holarctic distinctella group. The archaica group, listed in Kelley (1984), is dissolved here, with *iglesiassi* Gonzales and Terra transferred to subgenus *Oxyethira* (falcata group) and *elerobi* (Blickle) placed in incertae sedis. Two other species, *dunbartonensis* Kelley and *setosa* Denning, were earlier included in this subgenus (Kelley, 1984). Although they do bear similarities to species of this subgenus, the former is better considered a primitive offshoot from the lineage leading to this subgenus while the latter belongs to the subgenus *Oxyethira*. Males of subgenus *Holarctotrichia* are distinct from those of other subgenera in having a combination of long dorsolateral processes of segment VIII, convergent but not distally fused subgenital processes and an aedeagus with an elongate titillator. Females are characterized by the presence of a dorsal knob on tergum VIII, a small sternum VIII and divergent apodemes.

Type specimens are deposited in the following locations: Urbana, Illinois, USA—The Illinois Natural History Survey (*araya* and *serrata*); Lunz am See—Malicky personal collection (*archaica*); Helsinki, Finland—The Zoological Museum (*distinctella*); London, England—The British Museum (Natural History) (*forcipata* and *michiganensis*); St. Paul, Minnesota USA—The University of Minnesota Insect Collection (*obtusatus*); Zurich, Switzerland (*sagittifera*).

Subgenus *Holarctotrichia* Kelley

Figs. 1-4

Type Species.—*Oxyethira distinctella* Mac Lachlan, 1880.

Length: 2.4-3.5 mm. Spur Formula: 0-3-4. Wing: R4 and R5 not fused.



Male.—Antenna 28–40 segmented; with or without placoid sensilla. Venter VII with apico-mesal process. Segment VIII: venter deeply excised or not; dorsum deeply excised; pleuron with dorsolateral process subtended by excision, anteriorly protruded within segment VII. Segment IX: venter broadly rounded anteriorly, reaching to caudal end of segment VII; dorsum with anterior margin distinct and protruded anteriorly from pleuron but with posterior margin indistinct with reduced sclerotization; posterolateral process usually present on pleuron. Inferior appendages reduced to darkened, truncate margins of broad mesocaudal lobe on venter IX or lacking completely; setal lobes often elongate. Subgenital processes distally convergent but not fused; bilobed process with elongate lobes. Aedeagus usually lacking distal processes or membranous areas; titillator encircling aedeagus one-half time, reaching to two-thirds the distance to apex.

Female.—Antenna 23–25 segmented. Venter VI with apicomesal process. Tergum VIII short with dorsal setose knob overlapping tergum IX; apodemes elongate, divergent; sternum VIII short, broad, well sclerotized, protruded ventrally on each side. Tergum X short. Spermathecal sclerite in posterior region of segment VII; horizontal lamella squared anteriorly.

FORCIPATA GROUP

Male.—Antenna: 34–37 segments. Segment VIII: venter shallowly excised; dorsolateral process usually reduced. Segment IX: venter caudally setose. Inferior appendages: indistinct. Setal lobes elongate with several setae. Subgenital processes: distally convergent and blunt. Bilobed process with lobes narrowed apically.

Female.—Antenna: 23–26 segments. Segment VIII: tergum with mid-dorsal knob bearing peg-like setae; sternum flattened in lateral view.

Oxyethira forcipata Mosely, 1934

Male.—Antenna: 34–38 segments. Segment VIII: dorsolateral process short and blunt; pleuron not protruded into segment VII. Segment IX: anterodorsal margin concave; venter with caudomesal protuberance. Aedeagus: narrow-elongate with base in segment VI.

Female.—Antenna: 23–24 segments.

Distribution.—Southern Appalachians to Ontario and Wisconsin.

Oxyethira michiganensis Mosely, 1934

Male.—Antenna: 35 segments. Segment VIII: dorsolateral process broad basally with proximal spine and narrow-curved distally with elongate apical seta; pleuron deeply protruded into segment VII. Segment IX: anterodorsal margin rounded; venter broadly convex along caudal margin.

Female.—Antenna: 23–24 segments. Segment VIII: mid-dorsal knob nearly disconnected from remainder of tergum VIII.

Distribution.—Eastern Nearctic.

←
Fig. 1. Terminal abdominal segments of adult males of the subgenus *Holarctotrichia*; lateral view. bp—bilobed process, dp—dorsolateral process, ia—inferior appendages, pl—posterolateral processes, sg—subgenital process, sl—setal lobe.

***Oxyethira obtatus* Denning, 1947**

Male.—Antenna: 35 segments. Segment VIII: dorsolateral process long and narrow; pleuron shallowly protruded within segment VIII. Segment IX: antero-dorsal margin concave; mesocaudal margin concave and serrate. Aedeagus: apex tipped with a pair of minute spines.

Female.—Antenna: 24 segments.

Distribution.—Northeastern North America.

***Oxyethira serrata* Ross, 1938**

Male.—Antenna: 35–37 segments. Segment VIII: dorsolateral process stout and serrate along dorsal margin; pleuron deeply protruded within segment VII. Segment IX: anterodorsal margin rounded; venter caudally indistinct.

Female.—Antenna: 26 segments. Tergum X: broadened distally.

Distribution.—Eastern Nearctic.

DISTINCTELLA GROUP

Male.—Antenna: 28–39 segments. Segment VIII: venter excised at least one-half its length; dorsolateral process elongate with 3–4 distal teeth and subtended by deep excision. Segment IX: elongate posterolateral process. Inferior appendages: fused onto shallowly bifurcate median plate; setal lobes blunt. Subgenital processes: apically tapered.

Female.—Antenna: unknown. Segment VIII: sternum broad in lateral view.

***Oxyethira araya* Ross, 1938**

Male.—Antenna: 38 segments. Segment VIII: pleuron deeply protruded within segment VII. Segment IX: posterolateral process straight. Aedeagus: apex with spine.

Female.—Sternum VII not excised. Segment VIII: apodemes divergent.

Distribution.—Northeastern United States and maritime Canada.

***Oxyethira distinctella* Mac Lachlan, 1880**

Male.—Antenna: 28 segments. Segment VIII: pleuron deeply protruded within segment VII. Aedeagus: apex simple, without spine.

Female.—Sternum VII deeply excised. Segment VIII: apodemes divergent.

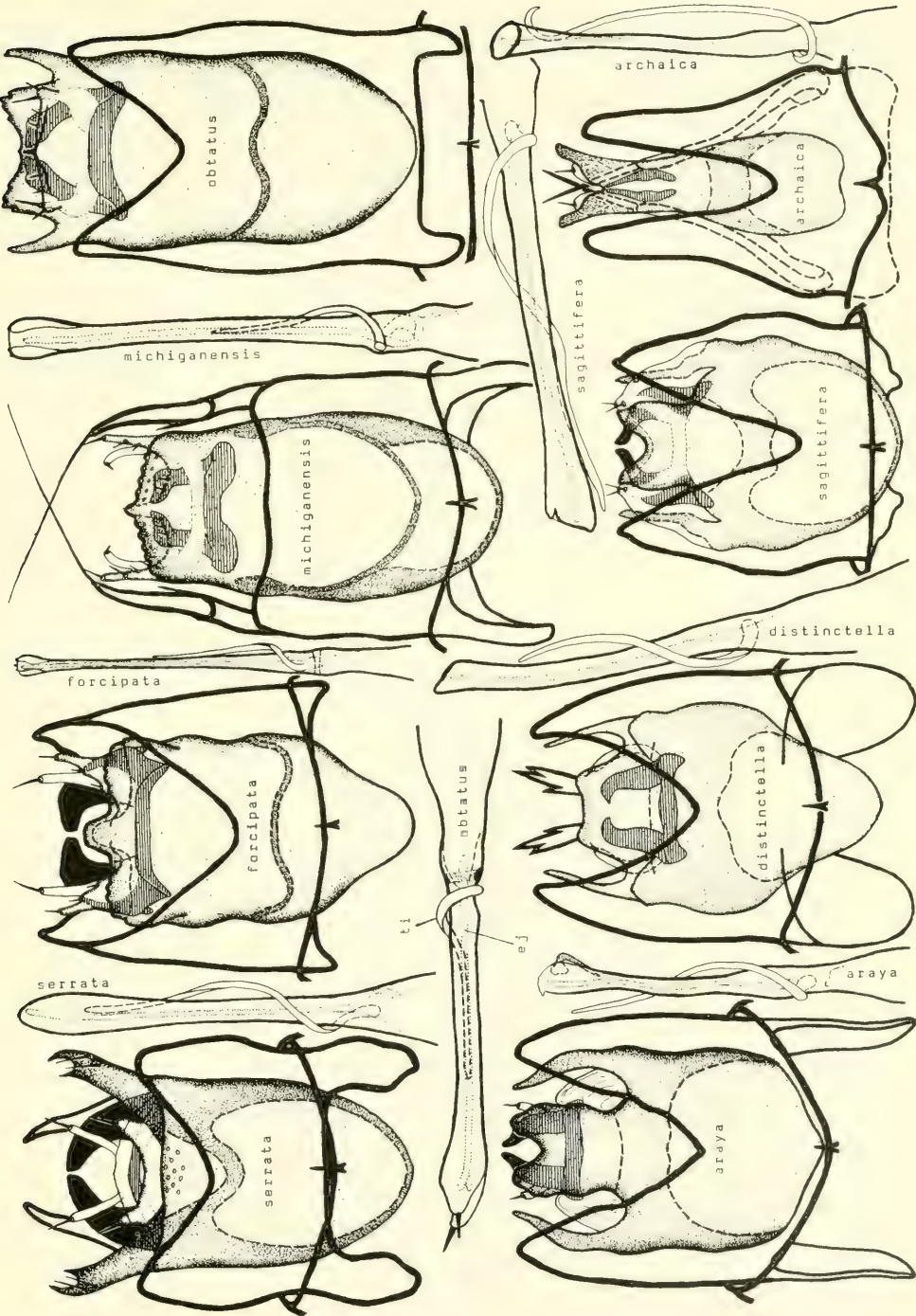
Distribution.—North and central Europe.

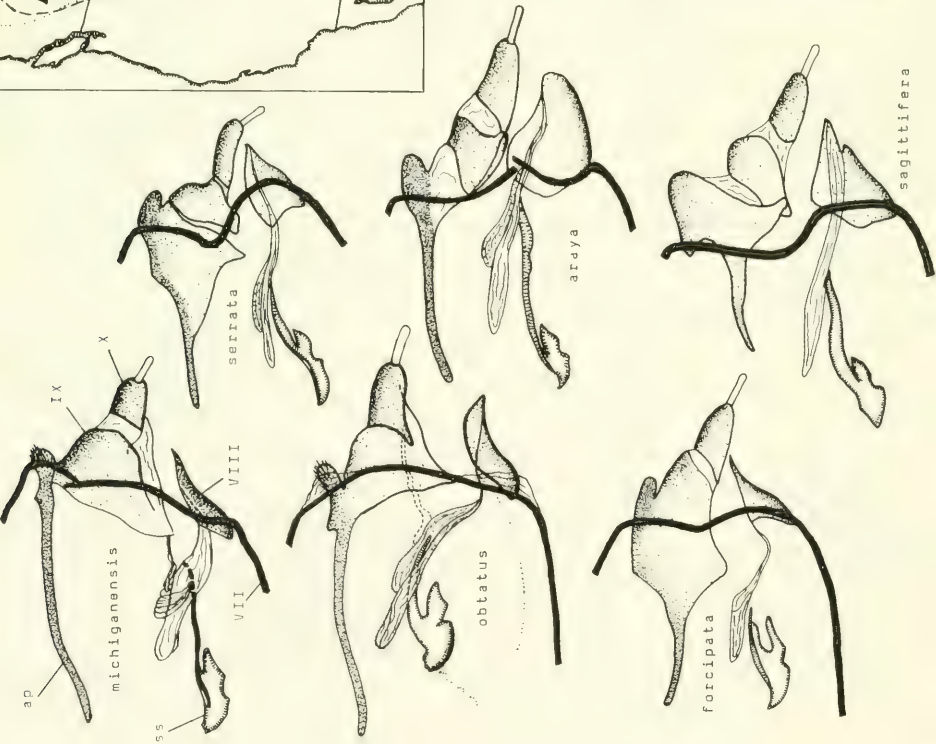
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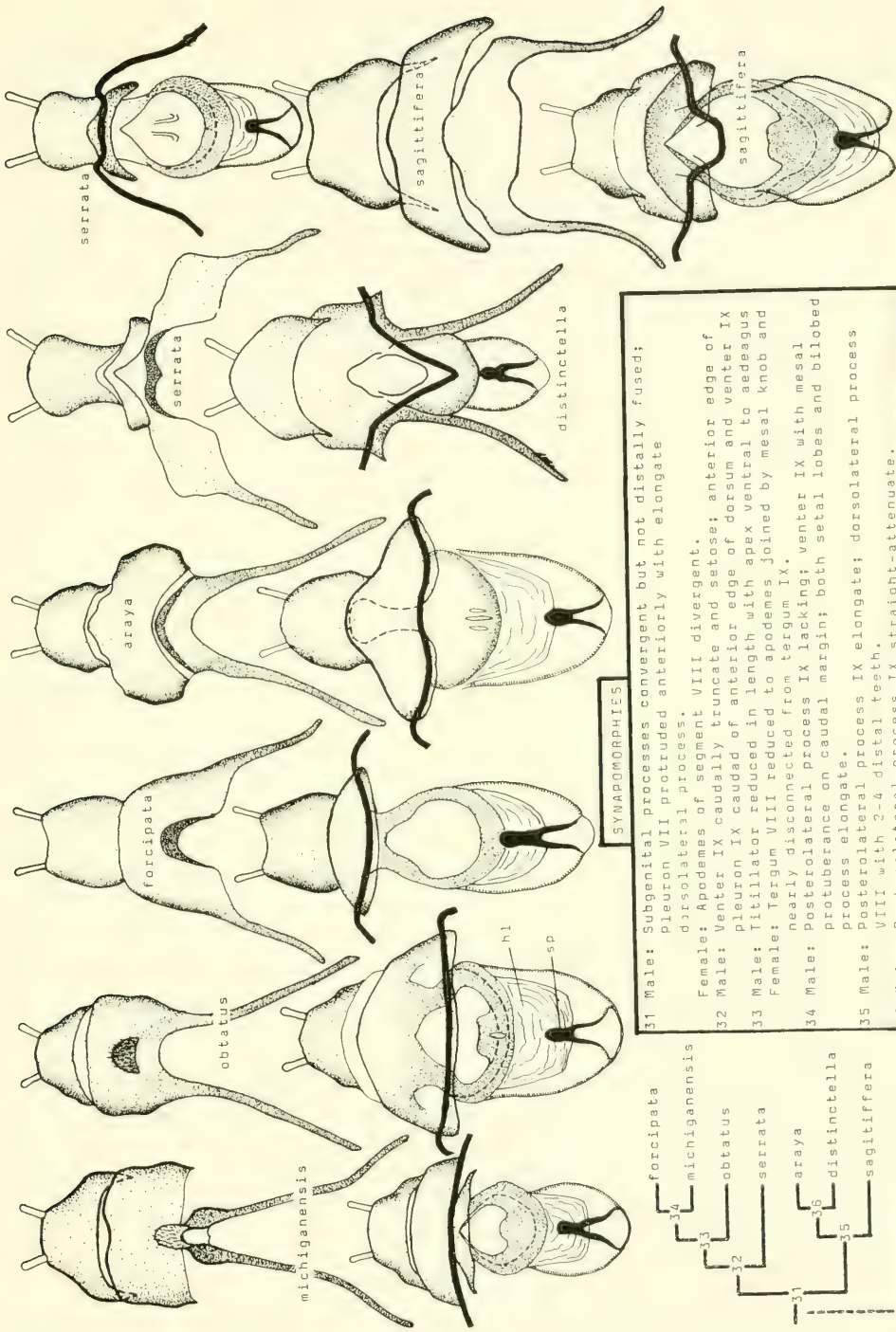
Fig. 2. Terminal abdominal segments of adult males of the subgenus *Holarctotrichia*; ventral view and aedeagus. ej—ejaculatory duct, ti—titillator.

Fig. 3. Terminal abdominal segments of adult females of the subgenus *Holarctotrichia* (lateral view) and maps of species distributions. ap—apodeme of segment VIII, ss—spermathecal sclerite.

Fig. 4. Terminal abdominal segments of adult females of the subgenus *Holarctotrichia* Kelley (dorsal view of segments VIII–X and ventral view including internal sclerites) and phylogeny of subgenus. hl—horizontal lamella, sp—spermathecal process.

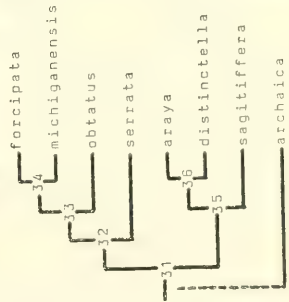






SYNAPOMORPHIES

31 Male: Subgenital processes convergent but not distally fused; pleuron VII protruded anteriorly with elongate dorsolateral process.
Female: Apodemes of segment VIII divergent.
32 Male: Venter IX caudally truncate and setose; anterior edge of pleuron IX caudad of anterior edge of dorsum and venter IX
33 Male: Filitillator reduced in length with apex ventral to aedeagus
Female: Tergum VIII reduced to apodemes joined by mesal knob and nearly disconnected from tergum IX.
34 Male: posterolateral process IX lacking; venter IX with mesal protuberance on caudal margin; both setal lobes and bilobed process elongate.
35 Male: posterolateral process IX elongate; dorsolateral process VII with 2-4 distal teeth.
36 Male: posterolateral process IX straight-attenuate.



Oxyethira sagittifera Ris, 1897

Male.—Antenna: 38–39 segments. Segment VIII: pleuron not protruded within segment VII. Segment IX: posterolateral process sinuate. Aedeagus: apex simple, without spine.

Female.—Sternum VII not excised. Segment VIII: apodemes nearly parallel.

Distribution.—North and central Europe.

UNPLACED TO SPECIES GROUP

Oxyethira archaica Malicky, 1975

Male.—Length 2.5–3.0 mm. Antenna: 40 segments. Dorsolateral processes elongate, proceeding ventrally and turning horizontally, tipped with one long spine; ventrolateral lobe narrow-elongate. Venter IX truncate anteriorly; dorsum a broad band. Inferior appendages with distolateral truncate processes. Subgenital processes hook-like in lateral view. Aedeagus widened distally; distal processes lacking; titillator recurved apically.

Female.—Those tentatively associated with this species seem more likely to be those of *Oxyethira iglesiassi* Gonzales & Terra, also from Portugal.

Distribution.—Portugal.

BIOGEOGRAPHY

Fig. 3

The subgenus *Holarctotrichia* is restricted to the Holarctic Region. Larvae show a distinct preference for lentic habitats, particularly lakes and ponds, although the larvae of *michiganensis* Mosely and *forcipata* Mosely may inhabit areas of slow current in rivers.

The *forcipata* group is nearctic and inhabits an area extending from northeastern United States south to the southern Appalachian Mountains and west to British Columbia. The northern limit of this endemic area is unknown but is probably related to temperature tolerance. A close correlation can be seen between the range of the *forcipata* group and the distribution of natural lakes in North America. This is particularly true of *serrata* and *obtatus*. The other two species, *forcipata* and *michiganensis*, exhibit a range extension into the southern Appalachians and their eastern foothills. It seems that this is due to adaptation by larvae of these two species to depositional areas of cold water rivers of the Appalachian mountains. They have not been collected from the many man-made reservoirs of southeastern United States.

Distributional patterns of the *distinctella* group are similar to those seen in the *forcipata* group. Two species are known from the palearctic region, *distinctella* and *sagittifera*. Both occur in northern Europe and the Alps, where natural lakes are abundant. A third species of the group, *araya*, occupies a small range from Ontario to New Brunswick. The larvae of *archaica* are known only from rivers in northern Portugal.

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NOTE

New Distribution Records for Some Nearctic Chalcidid Wasps
(Hymenoptera: Chalcididae)

Burks (*In* Krombein et al., 1979, Catalog of Hymenoptera in America North of Mexico, Vol. I (Parasitica), Smith. Inst. Press: 860–874) listed distribution information for each species of chalcidid wasp in America north of Mexico. Recently, I examined over 4000 chalcidid wasps from the Florida State Collection of Arthropods, Florida Department of Agriculture, Gainesville which yielded new distribution records for eight species. This information is presented because it contributes to the knowledge of the distribution of Nearctic Chalcididae by updating the distributional information in Burks (*Ibid.*). This new information includes one record for the United States, ten state records, and one record for Canada.

The new state records for these wasps, though not involving large discrepancies from their previously known distributions, are significant in expanding their distributions into these states. They are as follows: *Metadontia amoena* (Say) in Texas, *Spilochalcis coxalis* (Cresson) in Florida and Missouri, *Ceratosmicra debilis* (Say) in Montana, *Brachymeria compsilurae* (Crawford) in Florida and Oklahoma, *B. hammari* (Crawford) in Arizona, and *B. tegularis* (Cresson) in Florida, Idaho, and Minnesota.

Two new country records involve *Ceratosmicra meteori* Burks and *Brachymeria carinatifrons* Gahan. *Ceratosmicra meteori* is recorded for the first time in Canada at Newfoundland, Portland Creek near Daniel's Harbour, June 1974, G. H. Heinrich, Malaise trap (one female). Burks (*Ibid.*) listed the distribution of this wasp as Massachusetts south to North Carolina, west to Illinois, Louisiana, Texas, Washington and Mexico. Halstead (1986, Entomol. News 97: 99–100) added California, Arizona, and Florida.

Brachymeria carinatifrons is recorded for the first time inside the United States at Texas, Hidalgo County, Bentsen Rio Grande Valley State Park, near mission, 16–18 July 1981, C. Porter (two females). This wasp's previous distribution was Mexico and Brazil (Burks, 1960. Trans., Am. Entomol. Soc. 86: 225–273). *Brachymeria carinatifrons* might be expected in the United States as it is a parasite of two tachinid flies (*Paradexodes epilachnae* Aldrich and *Lydinolydella metallica* Townsend) which were introduced for the biological control of coccinellid beetles of the genus *Epilachna* (Burks, *Ibid.*).

I thank L. A. Stange and J. Wiley for the loan of chalcidid material. I also thank T. E. Esser, California Department of Food and Agriculture, Sacramento, N. J. Smith, Fresno County Agricultural Commissioner's Office, Fresno, California, and D. J. Burdick, California State University–Fresno, for editorial comments on this manuscript.

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NOTE

Striking Sexual Dimorphism and its Taxonomic Consequences among
New World Phorid Flies (Diptera)

On my recent visit to the Biosystematics Research Institute (BRI) in Ottawa, Ontario, D. M. Wood pointed out to me six wingless female phorid flies of the species *Trophodeinus barberi* Borgmeier, collected in the head of a Malaise trap near Ottawa. This genus is known from three species described from females only. Wingless females of the genus *Aenigmatias* Meinert are often found in Malaise heads with their associated winged males (pers. obs.), and recently Miller (1984. Ecol. Entomol. 9: 293-302) published accounts of wingless female *Puliciphora borinquenensis* Wheeler being carried in flight by males to new oviposition sites. As it was unlikely that the female *T. barberi* crawled to the apex of the trap, it was reasonable to assume that the hitherto unknown males should have been in the same samples. In the collection were seven male *Bactropalpus furcatus* Borgmeier, belonging to a genus known only from males, collected during the same time period in this Malaise trap. Matching the dates gave five pairs, plus two single males and a single female. The presence of the lone female can be attributed to overlooking a specimen of the small, nondescript male in a crowded Malaise residue. This association suggests that *T. barberi* and *B. furcatus* are the same species.

A second co-occurrence of these flies was noted from a flight intercept trap set in Coronado National Memorial, Arizona, where a pair belonging to an undescribed species were collected.

Borgmeier (1960. Studia Entomol. 3: 257-374) described *Trophodeinus* from Brazil, and later recognized two more species from North America (1963. Studia Entomol. 6: 1-256). The genus was recognized on the basis of the greatly enlarged proboscis, reduced eyes, and reduced frontal setation. *Bactropalpus* was erected by Borgmeier (1963. Rev. Bras. Biol. 23: 165-170) for a group of seven *Puliciphora*-like males (including *B. furcatus*) that share the characters of expanded, flattened palpi with short setae and complex, distinctive genitalia.

Based on the association of specimens in the Ottawa traps, the names *B. furcatus* and *T. barberi* are synonymous, with *B. furcatus* the junior synonym (NEW SYNONOMY). Although the type species of both *Bactropalpus* (*B. chelifera*) and *Trophodeinus* (*T. analis*) are Brazilian, the two species combined here exhibit, in common with these type species, all the diagnostic characters of the genera in which they were described. Therefore, the genera are also considered to be congeneric, and their names synonymous. The name *Bactropalpus* is a junior subjective synonym (NEW SYNONOMY), and the valid name for the genus is *Trophodeinus*.

The following species are transferred to *Trophodeinus* as NEW COMBINATIONS: *T. arizonensis* (Borgmeier) Arizona: Maricopa Co.; *T. chelifera* (Borgmeier) Brazil: Nova Teutônia, S.C.; *T. denticulatus* (Borgmeier) Texas: San Antonio; *T. lobatus* (Borgmeier) Brazil: Nova Teutônia, S.C.; *T. spatulatus* (Borgmeier) New Mexico: Catron Co.; *T. vicinus* (Borgmeier) Guatemala: Acatenango. The other

three species of *Trophodeinus* are: *T. analis* Borgmeier Brazil: Nova Teutônia; *T. barberi* Borgmeier Maryland: Plummer's Island; *T. pygmaeus* Borgmeier Michigan: Livingstone Co.

There seem to be few structural characters to associate the males and females of *Trophodeinus*, other than the frontal setae and the somewhat flattened, elongate hind basitarsus, but the highly derived condition of the male genitalia may be correlated with the unusual female genital segments. Nothing is known of their natural history, although a slide mounted female from the Ottawa collection shows that the proboscis ensheathes a long, thin stylet, suggesting a predatory habit. Males are commonly attracted to lights, and a male *T. spatulatus* from Arizona was collected with *Neivamyrmex* sp. (Hymenoptera: Formicidae).

The data for the Ottawa area specimens and new records for *T. furcatus* and *T. spatulatus* are listed below. All specimens are deposited at BRI, Ottawa (BRI) or the author's collection (BVB):

T. barberi. CANADA. Ontario: Metcalfe, 21.vii.1984, 1 ♂, 1 ♀, 24.vii.1984, 3 ♂, 4 ♀, 26.vii.1984, 2 ♂, 1.viii.1984, 1 ♂, 1 ♀, B. E. Cooper. (Malaise trap) (BRI). UNITED STATES. Arizona: Coconino Co., 20 mi. N. Flagstaff, Bonito Park, 8-25.viii.1984, 7000', B. V. Brown, intercept trap, ponderosa pine/meadow, 1 ♂ (BVB).

T. spatulatus. UNITED STATES. Arizona: Cochise Co., S.W.R.S. nr. Portal, 5400', 6.ix.1970, V. Roth, with army ants, riparian forest, 1 ♂ (BVB).

I acknowledge the helpful comments of G. E. Ball, K. N. Barber and S. A. Marshall.

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BOOK REVIEW

Fundamentals of Insect Physiology, Murray S. Blum, ed. John Wiley & Sons, New York. 1985. 598 pp. Cost: \$39.95 (hardbound).

Dr. Blum challenged fourteen contributors, including himself, to present a contemporary view of insect physiology "with lucid explications and meaningful syntheses . . . while at the same time emphasizing the multitude of questions that beg to be answered by tomorrow's research." By-and-large the contributors have successfully met their charge, some in outstanding fashion, to produce a textbook eminently suitable as a foundation for a course in insect physiology. The contents of the book are as follows:

Insect Physiology: Problems in Terminology (M. S. Blum, 3 pp.).

1. Circulatory System (J. P. Woodring, 53 pp.).
2. Nutrition and Digestive Organs (J. E. McFarlane, 31 pp.).
3. Excretory Systems (D. G. Cochran, 48 pp.).
4. The Integument (H. R. Hepburn, 45 pp.).
5. Respiratory Systems (J. L. Nation, 41 pp.).
6. Muscle Systems (T. Smyth, Jr., 26 pp.).
7. Nervous System: Electrical Events (D. L. Shankland and J. L. Frazier, 34 pp.).
8. Nervous System: Sensory System (J. L. Frazier, 70 pp.).
9. Nervous System: Functional Role (J. L. Eaton, 34 pp.).
10. Behavioral Physiology (W. R. Tschinkel, 45 pp.).
11. Reproductive Systems (S. J. Berry, 30 pp.).
12. Intermediary Metabolism (S. Friedman, 39 pp.).
13. Hormonal Action During Insect Development (H. Oberlander, 28 pp.).
14. Exocrine Systems (M. S. Blum, 45 pp.).

Each chapter has its own summary, detailed table of contents with page references to numbered sections, conclusion suggesting areas fertile for future research, and reference list. There is an eighteen-page index, including insect genera and chemical compounds.

Blum defines various metamorphic terms in his opening statement, stressing the clarification made by Hinton (to whom the book is dedicated) that a molt consists of apolysis and ecdysis. This brief terminological discourse lends cohesion to discussions of metamorphic events in the rest of the book. Unfortunately, though, the term "instar" will continue to be confusing because Blum states that instar refers "to both the time interval between ecdyses (so does the word stadium) and the individual between ecdyses" while J. C. Jones (Ann. Entomol. Soc. Am. 71: 491) argued that "instar represents the individual during the period between apolyses, and the stage is the period in an arthropod's life between ecdyses." The latest definition of instar by the Entomological Society of America (J. Econ. Entomol. 78(4): v.) side-steps the issue; "Instar. The arthropod itself between two successive molts [and] . . . hatching is considered a molt."

Tschinkel's chapter on Behavioral Physiology and Frazier's chapter on the Nervous System: Sensory System are, in my opinion, outstanding contributions.

The "automation" view of insects is dispelled by Tschinkel through critical appraisals of well-chosen examples. He stresses the importance of analysis of variance and appropriate control experiments in deciphering the often subtle interactions between physiology and behavior, concluding that "For the lover of terra incognita, the place to be is the effect of behavior on physiology." Frazier's chapter is the longest in the book, but is well written and illustrated, including several superb scanning electron micrographs of sensilla. He presents and clearly explains the new terminology for insect sensilla, and draws largely upon recent, primary references to discuss insect sensory modalities.

The chapters on Muscle Systems and Reproductive Systems are weak. References to recent physiological work on insect muscle are lacking. The description of muscular physiology is difficult to follow and the few illustrations do little to make the task easier. The chapter on Reproductive Systems is too superficial even for a general text. I think it unfortunate that Berry chose not to give more detailed coverage of "the rich array of imaginative and sometimes bizarre reproductive mechanisms found in nature." Although an accurate account of the general scheme of insect reproduction is presented (using mostly figures of silkmoths), this chapter will not capture the imagination of students as I think it could have.

The remaining chapters are all solid contributions with ample references and illustrations. I particularly enjoyed the enthusiastic writing styles of Hepburn (The Integument) and Blum (Exocrine Systems). Blum's comparative approach to insect allomones and pheromones, complete with chemical structures, successfully conveys the message that insects are "natural products chemists par excellence." Friedman's chapter is noteworthy for its well-written introduction and conclusion tying together an in-depth treatment of intermediary metabolism using balanced chemical equations. Oberlander gives an excellent history of insect neuroendocrine research and a very readable explanation, albeit somewhat deficient in detail, of the endocrine control of insect development.

Perhaps unavoidably the information in the book is already five years out-of-date, limiting its usefulness as a reference for specialists. For example, no mention is made of recent discoveries that insects acetylate rather than oxidize their biogenic amines, that JHI and II occur only in Lepidoptera, or that not all insects use 20-hydroxyecdysone as their molting (apolysing) hormone. However, *Fundamentals of Insect Physiology* is still an excellent companion text for a course in insect physiology.

Jeffrey R. Aldrich, *Insect and Nematode Hormone Laboratory, Agricultural Research Service, USDA, Beltsville, Maryland 20705.*

BOOK REVIEW

A Scanning Electron Microscope Atlas of the Honey Bee, by E. H. Erickson, Jr., S. D. Carlson, and M. B. Garment. The Iowa State University Press, Ames. 1986. 292 pp., illus. Cost: \$49.95 (hardbound).

This glossy, $9 \times 12\frac{1}{2}$ inch, coffee-table volume consists primarily of numerous plates composed of scanning electron micrographs that show the externally exposed body parts of the honey bee castes. The book has a concise six-page introduction that includes some startling information on the history, biology and use of honey bees. For example, "A single worker larva is fed approximately 1300 meals per day for 5 days . . ." or, "A typical colony may use up to 100 lb. pollen for brood rearing each year; 4 million foraging trips are required to collect this quantity," or ". . . foraging bees get about 11,265,100 km (7 million flight miles) to 3.8 L (1 gal.) honey." The book is divided into three sections dealing with micrographs of the queen, the workers and the drones, each with its own brief but interesting introduction.

Most micrographs are of good quality (exceptions mainly are the photomontages). They illustrate the beautiful sculpturing and intricate, varied detail common to insects that we normally can neither see nor appreciate. The external morphology of insects is particularly suitable for examination by scanning electron microscopy and this book provides a good, semipopular introduction.

If this reviewer were preparing this book, alterations would be made to enhance reader comprehension and aesthetics. For example, the sequence of several legends seems haphazard (such as those on pp. 41, 53, 65, 95, 115, 129, 133). Each micrograph should have a number, referred to in the legend, as required in most scientific journals. A greater use of modest arrows or letters to correlate the illustrated parts with their descriptions would have been helpful. About half of each page that bears legends (facing the plates) is blank, wasted space; it would have been most helpful to include there small, labelled, diagrammatic *in situ* drawings of each body part that is illustrated and discussed. Flipping back to the generalized drawings in the appendix is not convenient and may confuse nonspecialists. Where possible, micrographs of body parts of all castes should have been from the same angle and at the same magnification, and it would have been preferable for easy comparison to include the same shared body parts of each caste (for example, the glossa of queen, worker and drone) on the same plate, instead of illustrating each caste in a separate section. A useful glossary of morphological terms, an index, and a brief list of references are included.

Suzanne W. T. Batra, *Systematic Entomology Laboratory, BBII, Agricultural Research Service, USDA, BARC-West, Beltsville, Maryland 20705.*

BOOK REVIEW

Handbook of Insect Rearing. Vols. I and II, Pritam Singh and R. F. Moore, eds. Elsevier Science Publishers, Amsterdam, The Netherlands. 1985. 488 pp., and 514 pp. Cost: \$96.00.

This two volume set is intended as a standard book to provide guidelines for rearing insects. The senior author developed a "cookbook style" for presentation of information. This format was circulated to prospective contributors. The information is generally provided in 8 sections—introduction, facilities and equipment, diet or food, rearing and colony maintenance, insect holding, life cycle, supply procedure, and references. The authors have succeeded admirably in obtaining a somewhat uniform format. However, the rearing techniques are the individual cooperators' methods, not necessarily standard methods. Standard methods should be developed, preferably by a committee whose members are familiar with the rearing techniques.

Volume I consists of a series of general articles on rearing. There are sections on diets, both natural and artificial, diseases, quality assessment, design of rearing facilities, and insect rearing management. These are followed by species-specific rearing procedures for Coleoptera, Collembola, Dictyoptera, Hemiptera, Hymenoptera, Neuroptera and Orthoptera.

Volume II follows the same pattern as the previous volume, covering the orders Diptera and Lepidoptera. Both volumes contain an index to common names and scientific names.

Though the authors recognize that they were under constraints as to selecting contributors and selecting which species should be discussed, it becomes rather evident that the selection process may have had an unintentional bias. Agricultural insect rearing techniques far outnumber those of medical/veterinary importance. For example, no mention is made of rearing techniques for *Anopheles* mosquitoes, a vector of a major disease. Three of the four species of mosquitoes discussed are techniques used at Notre Dame University, which, though excellent and perfectly adequate for research at that university, do not necessarily reflect the rearing techniques used at other facilities. It would have been better to have assigned different species to four or five rearing facilities. No mention is made of rearing Anoplura (i.e. *Pediculus humanus*), or Siphonaptera (i.e. *Ctenocephalides felis*), or bedbugs (*Cimex* sp.) or any of the tick species (granted they are not insects). Another rearing technique omitted is for the rather commonly reared insect, the small milkweed bug (*Lygaeus kalmii*). Surprisingly, mealworm (*Tenebrio* sp.) rearing is omitted from the order Coleoptera.

The two volumes will be a handy adjunct to any facility that rears or intends to rear insects. The "cookbook style" of rearing instructions is excellent. The listing of the sources of supplies with addresses is extremely helpful. The list of references at the end of each rearing technique could have been expanded. It is hoped that a much more complete volume will be produced that would fill the gaps in the present volumes.

Eugene J. Gerberg, *Insect Control & Research, Inc.*, 1330 Dillon Heights Ave., Baltimore, Maryland 21228.

SOCIETY MEETINGS

919th Regular Meeting—January 2, 1986

The 919th Regular Meeting of the Entomological Society of Washington was called to order by President Edward M. Barrows in the Naturalist Center, National Museum of Natural History, at 8 p.m. on January 2, 1986. Twenty-one members and three guests were present. Minutes of the previous meeting were read and approved. The treasurer's report was read and approved and the Auditing Committee report was read. President Barrows introduced Michael J. Raupp, the new Program Committee Chairman. Membership Chairman, Geoffrey White, read the names of the following applicants for membership: Michael R. Wagner, Flagstaff, Arizona; David D. Zeigler, Denton, Texas; Nathan Erwin, Crofton, Maryland; and John D. Plakidas, Germantown, Maryland.

Under new business, T. E. Wallenmaier discussed the June banquet and asked for suggestions about where to hold the banquet and possible speakers.

No old business was presented for discussion.

C. W. Sabrosky displayed beautifully mounted butterflies made in Taiwan.

T. Wallenmaier reported on a recent publication, *Butterflies and Moths of Great Britain*, and passed a copy around for viewing.

The speaker of the evening was Michael Schauff, Research Entomologist, Systematic Entomology, USDA, Washington, DC. His talk was entitled "Chalcidflies: A Brief Look at the Past, Present and Future." Chalcidoid wasps are a poorly known group distinguished by a remarkable diversity of morphology, biology, and size. The current classification is largely that of early workers with numerous subgroups that have been elevated or sunk in rank. A combination of new technologies and the study of new characters is pointing out the need for some radical changes in the classification of this large and economically important group of insect parasites.

Following the introduction of guests and the announcement of the illness of several members, the meeting was adjourned at 9:15 p.m. Refreshments followed.

Paul M. Marsh, *Recording Secretary*

920th Regular Meeting—February 6, 1986

The 920th Regular Meeting of the Entomological Society of Washington was called to order by President E. M. Barrows in the Naturalist Center, National Museum of Natural History, at 8 p.m. on February 6, 1986. Twenty-one members and five guests were present. Minutes of the previous meeting were read and approved. The Corresponding Secretary, R. G. Robbins, presented a report on the membership of the Society. The membership numbers 632; these are located in 48 states and Puerto Rico, and 61 are foreign. The state with the largest number of members is Maryland followed by District of Columbia, California, Virginia, Florida and New York.

T. Wallenmaier reported that details of the Spring banquet were not yet settled but will be reported at the next meeting.

Membership Chairman, G. White, read the names of the following applicants for membership: Tim A. Christiansen, Laramie, Wyoming; Paul S. Cwikla, Columbus, Ohio; Yuen-Shaung Ng, Woodbridge, Virginia; John R. Spence, Edmonton, Alberta; Warren G. Abrahamson, Lewisburg, Pennsylvania.

No old or new business was presented for discussion.

The speaker of the evening was Donald M. Anderson, Research Entomologist, Systematic Entomology Laboratory, USDA, Washington, DC. His talk was entitled "Dodder weevils: their hosts and relatives, an intriguing but entangled problem." Species in the genus *Smicronyx* display a variety of biologies: some are associated with parasitic plants called dodders, others with parasitic plants in the Scrophulariaceae and Orobanchaceae, still others with Asteraceae and Gentianaceae, which are not parasitic. The dodder-loving species include a local species with an unusual life cycle in which the larvae feed in the stems of dodders and also in the asteraceous hosts of the dodders. The significance of these facts is still unclear, but the potential of the problem for significant research seems very high.

Following the introduction of guests, the meeting was adjourned at 9:15 p.m. Refreshments followed.

Paul M. Marsh, *Recording Secretary*

921st Regular Meeting—March 6, 1986

The 921st Regular Meeting of the Entomological Society of Washington was called to order by President Edward M. Barrows in the Naturalist Center, National Museum of Natural History, at 8 p.m. on March 6, 1986. Sixteen members and three guests were present. Membership Chairman G. White read the names of the following applicants for membership: Atilano Contreras-Ramos, Monterrey, Nuevo Leon, Mexico; John M. Heraty, Department of Environmental Biology, University of Guelph, Ontario; Steve L. Heydon, Illinois Natural History Survey, Champaign; Peter W. Price, Department of Biological Sciences, Northern Arizona University, Flagstaff; Barbara J. Sheffer, Zoology-Entomology Department, Auburn University, Alabama; Joseph D. Shorthouse, Department of Biology, Laurentian University, Sudbury, Ontario; Terry A. H. Stasny, Morgantown, West Virginia; Gwendolyn W. Waring, Department of Biological Sciences, Northern Arizona University, Flagstaff; James B. Woolley, Department of Entomology, Texas A & M University, College Station; and Wu Yar, Department of Biology, Georgetown University, Washington, D.C.

President Barrows exhibited nesting tubes for orchard bees and literature on these insects.

R. J. Gagné reported that the Executive Committee has agreed to increase institutional subscription rates in anticipation of increases in publication costs for the *Proceedings*. The new rates, to take effect in 1987, will be \$35 per year for domestic subscriptions and \$40 per year for foreign subscriptions. It is also the sense of the Executive Committee that membership dues should now be increased, preferably to \$20 per year, in order to counter recent declines in Society reserves. The membership was asked to consider this proposal with a view to voting on it at a future meeting.

R. G. Robbins reported the death on 24 February of Harry Hoogstraal, the world's foremost authority on ticks and tickborne diseases and a member of this Society since 1946. Dr. Hoogstraal's scientific productivity was superhuman: he personally authored over 500 research papers and books, compiled a seven-volume tick bibliography containing over 80,000 references, and edited some 2,000 translations of the world tick literature. The recipient of dozens of honorary degrees, medals and awards, as well as the affectionate respect of countless colleagues, Dr. Hoogstraal died at his home in Maadi, a suburb of Cairo, Egypt, after a three-month battle with lung cancer. The Harry Hoogstraal Memorial Fund has been established in his memory. Contributions should be sent to the Department of Entomology, Smithsonian Institution, NHB 105, Washington, D.C. 20560.

The speaker for the evening was George B. Chapman, Chairman, Department of Biology, Georgetown University, Washington, D.C. His talk was entitled "Ultrastructural Features of the Cells of DuFour's Gland." This gland is associated with the sting in female Aculeata but does not produce toxin. Its exact functions are unknown but it is perhaps the richest source of natural compounds, especially hydrocarbons, in insects. Cells of this gland are remarkable for their reduced Golgi apparatus. Electron micrographs were presented contrasting the anatomy and cellular organelles of DuFour's glands extracted from carpenter and horn-faced bees.

The meeting was adjourned at 9:30 p.m. after which refreshments were served.

Richard G. Robbins, *Corresponding Secretary*

922nd Regular Meeting—April 3, 1986

The 922nd Regular Meeting of the Entomological Society of Washington was called to order by President E. M. Barrows in the Naturalist Center, National Museum of Natural History, at 8 p.m. on April 3, 1986. Twenty-one members and eight guests were present. Minutes of the previous two meetings were read and corrected. Membership Chairman, G. White, read the names of the following applicants for membership: Mary Jo Molineaux, Cheverly, Maryland, and P. Juliette Weinstein, Chevy Chase, Maryland.

T. Wallenmaier announced that the annual Spring banquet will be held on Friday, June 6, at the Continuing Education Center, University of Maryland. The Master of Ceremonies will be Lloyd Knutson; the guest speaker will be Bob Hedlund of the USDA who will speak on entomological projects around the world.

President Barrows called for the Treasurer's report. Because the Treasurer was absent, a discussion was held on the proper procedure to present a dues increase to the Society. Since this involved a change in the By-laws and must be presented in writing to the membership at the meeting before voted upon, President Barrows placed the amendment before the meeting in writing on the chalk board. The amendment proposes to raise annual membership dues to \$20, with \$2 of this going to membership and \$18 to subscription. The amendment will be voted upon at the next regular meeting, May 1, 1986.

No new or old business was presented for discussion.

T. J. Spilman displayed specimens of Palm Sunday beetles, *Hemipeplus marginipennis* and *H. chaos*. Living adults of both species and larvae of the latter

were collected from *Sabal palmetto* leaflets that were used in Palm Sunday liturgical services at Little Flower Church in Bethesda. The palm leaves had been harvested in Florida. The very flat adults and larvae live between leaflets of fronds that are in the spear stage. T. Spilman also displayed three new publications: *Israel National Collections of Natural History*, by Ilana Ferber; *Insects of Eastern Forests*, by USDA Forest Service, which discusses common forest pests and their habits and damage; and *An English Translation of Russian Common Names of Agricultural and Forest Insects and Mites*, by USDA Forest Service, presents the English names translated from Cyrillic, arranged by order and family, by scientific name alphabetically, and by translated common name alphabetically.

The speaker of the evening was Dr. James S. Miller, Postdoctoral Fellow, Department of Entomology, Smithsonian Institution. His talk was entitled "Evolution of host plant associations in swallowtail butterflies."

Following the introduction of guests, the meeting was adjourned at 9:30 p.m. Refreshments followed.

Paul M. Marsh, *Recording Secretary*

923rd Regular Meeting—May 1, 1986

The 923rd Regular Meeting of the Entomological Society of Washington was called to order by President E. M. Barrows in the Naturalist Center, National Museum of Natural History, at 8 p.m. on May 1, 1986. Twenty-four members and two guests were present. Minutes of the previous meeting were read. Membership Chairman, G. White, read the names of the following applicants for membership: Jonathan Mawdsley, Lynchburg, Virginia; Margery G. Spofford, Syracuse, New York.

T. Wallenmaier reminded the audience of the June banquet to be held June 6 at the University of Maryland. Tom asked about using Society funds to support a door prize at the banquet. It was decided that this was a matter for the Executive Committee and that he should canvass the committee members about this.

A vote was taken on the proposal presented at the previous meeting to raise Society dues. The vote count was 17 for, 0 against, 1 abstention, and President Barrows declared the vote unanimously passed.

M. Davis displayed a copy of the Bishop Museum News which contained pictures and articles about W. D. Duckworth. She showed also a copy of the recent issue of the Journal of the New York Entomological Society dedicated to Richard Froeschner on the occasion of his 75th birthday.

The speaker for the evening was Dr. David Dussourd, University of Maryland. His talk was entitled "Vein cutting: an insect counterploy to the latex defense of plants." Many herbivorous insects on latex-producing plants sever leaf veins before feeding beyond the cuts. Vein severance ruptures latex tubes, thus eliminating latex flow to the insect's feeding site.

Following the introduction of guests, the meeting was adjourned at 9:30 p.m. Refreshments followed.

Paul M. Marsh, *Recording Secretary*

924th Regular Meeting—June 6, 1986

The annual banquet of the Entomological Society of Washington and the Pest Science Society of Washington was held on June 6, 1986, in the Center of Adult Education, University of Maryland, College Park. After a social hour, dinner began at 7:30 p.m. The Master of Ceremonies was Lloyd Knutson, Biosystematics and Beneficial Insects Institute, Agricultural Research Service. The guest speaker for the evening was Robert Hedlund, Office of International Cooperation and Development, U.S. Department of Agriculture. His illustrated talk was entitled "Entomology: Passport to the World" and described the wide-ranging scope of entomology research in various parts of the world.

Paul M. Marsh, *Recording Secretary*

NOTICE TO MEMBERS AND SUBSCRIBERS

Due to increasing costs of postage and production of the *Proceedings*, the society has found it necessary to raise prices for subscriptions and annual dues for members. For 1987, dues for membership will be \$20.00. Subscriptions to U.S. institutions will be \$35.00 for 1987, and foreign subscriptions will increase to \$40.00.

Members are requested to pay their dues promptly, as very late renewals increase cost to the society when it is necessary to mail issues of the journals after the normal mailing occurs.

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No. 11. A Systematic Study of the Japanese Chloropidae (Diptera), by Kenkichi Kanmiya. 370 pp. 1983.....	18.00
No. 12. The Holarctic Genera of Mymaridae (Hymenoptera: Chalcidoidea), by Michael E. Schauff. 67 pp. 1984.....	5.00

Back issues of the Proceedings of the Entomological Society of Washington are available at \$25.00 per volume to non-members and \$13.00 per volume to members of the Society.

Prices quoted are U.S. currency. Postage extra except on prepaid orders. Dealers are allowed a discount of 10 per cent on all items, including annual subscriptions, that are paid in advance. All orders should be placed with the Custodian, Entomological Society of Washington, c/o Department of Entomology, NHB 168, Smithsonian Institution, Washington, D.C. 20560.

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